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THE MECHANISM OF FLUID ABSORPTION AT ECDYSIS IN THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*

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SUMMARY

1. The mechanism of fluid absorption at ecdysis was investigated in the stenohaline marine decapod, *Homarus americanus*.

2. Sea-water uptake began approximately 1 h before ecdysis, increased rapidly during ecdysis, and was completed 2 h after ecdysis.

3. Increased drinking rates were measured during and just after ecdysis. The quantity of water ingested was equal to the total amount of water absorbed during moult, indicating that fluid entered the haemolymph exclusively via the lining of the digestive tract.

4. It was estimated that 91% of the ingested sea water appeared in the haemolymph by 2·5 h postecdysis.

5. The midgut appeared to be the principal part of the digestive tract involved in the absorption of fluid into the haemolymph. X-radiography of lobsters that ingested a suspension of barium sulphate during ecdysis demonstrated that accumulation and concentration of this compound occurred within the midgut during the 2·5 h of haemolymph expansion following ecdysis. Elevated net water fluxes across perfused midgut were observed in late proecdysis and 0·5 h after ecdysis.

INTRODUCTION

In aquatic arthropods, shedding of the exuvium at ecdysis is accompanied by a rapid increase in wet weight as a result of water uptake (Olmsted & Baumberger, 1923; Drach, 1939; Lowndes & Panikkar, 1941; Corrivault & Tremblay, 1948; Travis, 1954; Robertson, 1960; Born, 1970; Dall, 1974). Uptake of water leads to an increase in haemolymph volume; diluting blood constituents and providing space for subsequent addition of tissue mass (Drilhon, 1935; Drach, 1939; Hollett, 1943; Robertson, 1960; Glynn, 1968; Barlow & Ridgway, 1969; Born, 1970; Bursey & Lane, 1971; Dall, 1974; Hepper, 1977).

Most authors agree that the gut lining is the major surface for water absorption (Drach, 1939; Passano, 1960; Robertson, 1960; Mykles & Ahearn, 1978). However, other investigators present qualitative evidence that the gills and/or general body surface are the primary absorptive surfaces at moult (Travis, 1954; Dandrifosse, 1966;

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Bocquet-Védrine, 1976). But previous studies have not presented quantitative information comparing the amount of water absorbed via a particular route to total water uptake, and thus the relative contribution of a specific absorptive surface to water uptake at moult is not known.

It is generally thought that water is driven across the lining of the digestive tract by osmotic and hydrostatic pressures (Passano, 1960; Robertson, 1960). In the mechanism proposed by Passano, blood osmotic pressure is said to increase as the animal approaches moult. At ecdysis, 'water is swallowed, increasing the hydrostatic pressure in the digestive tract lumen, and the combined effects of filtration and osmotic uptake cause water to pass into the hemolymph' (Passano, 1960, p. 492).

It would appear that the filtration-osmotic theory of Passano (1960) is not applicable to all decapod crustaceans. Elevated blood osmolalities during proecdysis have been observed only in strong osmoregulators such as *Pachygrapsus crassipes* (Baumberger & Olmsted, 1928), *Callinectes sapidus* (Baumberger & Dill, 1928), *Carcinus maenas* (Robertson, 1960), and *Eriocheir sinensis* (De Leersnyder, 1967). In contrast, blood osmolalities of stenohaline marine forms, such as *Homarus gammarus* (= *vulgaris*) (Lowndes & Panikkar, 1941; Glynn, 1968), *Pugettia producta* (Born, 1970), and *Penaeus duorarum* (Bursey & Lane, 1971), remain essentially iso-osmotic to sea water during the moulting cycle. Therefore, in many marine decapods, the absorption of water into the haemolymph is accomplished in the absence of any obvious osmotic gradient between blood and environment. For this reason, Born (1970) and Smith (1976) have hypothesized that water absorption is linked to active salt transport, which establishes local osmotic gradients at or just beneath the absorptive surfaces. The American lobster, *Homarus americanus*, is a poor osmoregulator (Dall, 1970). The present investigation examines the dynamics of fluid absorption in this species. It establishes the surface across which fluid is absorbed into the haemolymph and suggests a mechanism by which fluid absorption is accomplished.

MATERIALS AND METHODS

Juvenile American lobsters (1–13 g), *Homarus americanus* Milne Edwards, were raised in the aquaculture facility at the Bodega Marine Laboratory. Lobsters were fed food pellets and live brine shrimp (*Artemia*) and maintained at 19 ± 1 °C. The intermoult interval under these conditions was 3–8 weeks. All experiments were performed at room temperature (20 ± 2 °C).

Animals were weighed periodically as they approached and completed ecdysis. To determine the total amount of water absorbed (W_3) at moult, the following equation was employed (Travis, 1954):

$$W_3 = W_2 - (W_1 - E),$$

where W_1 is weight in late premoult (stage D_3; see below), W_2 is the weight after completion of water uptake in the postmoult period, and E is the wet weight of the exuvium. For purposes of comparison, these values were expressed as percentages of the premoult weight.

For determination of haemolymph osmolality, approximately 0·2 ml of blood was withdrawn from the ventral sinus. Whole blood and sea-water osmolalities were determined with an Osmette Precision Osmometer (Precision Systems, Inc.).

Measurement of drinking rate was made on lobsters placed in a 200 ml sea-water bath containing 25 μCi [^{14}C]inulin (inulin-carboxyl-^{14}C; ICN, 1·4 μCi/mg) for 1 h. After exposure, individuals were rinsed in unlabelled sea water and frozen. A 1 ml sample of labelled bath was taken at each exposure. While still frozen, the entire gut was removed and placed in a tared scintillation vial, dried to a constant weight at 60–70 °C, and weighed to the nearest 10^{-4} g. Distilled water (1 ml) was added to each vial to hydrate the tissue sample. Gut tissue was solubilized with 5 ml Protosol (New England Nuclear) at 50 °C for approximately 8 h, cooled to room temperature, and decolourized with 3% hydrogen peroxide (25 drops) at 50 °C for 30 min. Aquasol (NEN; 10 ml) was added to each vial, which was set aside for 12 h before counting. Protosol (5 ml), hydrogen peroxide (25 drops), and Aquasol (10 ml) were added to the vials containing the 1 ml samples of labelled bath. All samples were counted in a Packard Tri-Carb liquid scintillation spectrometer.

For measurement of haemolymph volume, lobsters were injected in the cardiac region with 10 μl of a solution containing [^{14}C]inulin (25 μCi/ml H_2O). After 30 min, a 1 ml bath sample was taken and a sample of blood withdrawn from the ventral sinus. The blood sample was weighed to the nearest 10^{-4} g to estimate sample volume, then digested with 1 ml Protosol at 50 °C for 15–30 min. Samples were cooled to room temperature and combined with 5 ml distilled water and 10 ml ScintiVerse (Scientific Products). Protosol (1 ml), distilled water (5 ml), and ScintiVerse (10 ml) were added to the vials containing the 1 ml bath samples and 10 μl samples of the [^{14}C]inulin solution. Haemolymph volumes (V) were calculated using the equation (Woodbury, 1974):

$$V = \frac{Q_a - Q_L}{C},$$

where Q_a is the quantity of radioactivity administered (cpm), Q_L is the quantity of radioactivity lost to the bath (cpm), and C is the concentration of radioactivity in the blood sample (cpm/ml).

X-radiography was performed on lobsters that had ingested a suspension of barium sulphate. Individuals undergoing ecdysis or immediately following ecdysis (stage A_1') were placed in a 500 ml sea-water bath containing 30 g $BaSO_4$ kept in suspension by vigorous aeration. After an exposure of variable duration (20–65 min), animals were periodically X-rayed with a Picker Industrial Mini-Shot X-ray unit at 80 kV for 10 s (source-to-target distance = 65 cm).

The measurement of transepithelial net water transport employed the method of Burg & Orloff (1968) as modified for the midgut of freshwater prawn (Ahearn *et al.* 1977; Mykles & Ahearn, 1978). The entire midgut was removed from each lobster and flushed with lobster saline to remove faecal material. The saline, modified from Welsh, Smith & Kammer (1968), contained, in mM: NaCl, 462·8; KCl, 15·7; $CaCl_2$, 25·9; $MgCl_2$, 8·3; Na_2SO_4, 8·4; D-glucose, 5·0; Tris-HCl (pH 7·4), 5·0 (995 m-osmol/kg H_2O).

The midgut was mounted on blunted 20-gauge syringe needles in a lucite chamber containing 10 ml saline as serosal bath and perfused with saline at approximately 100 μl/min by means of a peristaltic pump (Sage Instruments). To determine the magnitude and direction of net water transport, the difference in perfusate concen-

tration of radioactively labelled non-absorbed volume marker ([^{14}C]inulin) before and after passage through the midgut was measured.

The perfusion rate, V_0 (μl/min), was calculated as:

$$V_0 = \frac{^{14}C_{tot}}{^{14}C_0\,(t)},$$

where $^{14}C_0$ is the radioactivity of the perfusion fluid (cpm/μl), $^{14}C_{tot}$ is the total radioactivity of the collected perfusate (cpm), and t is the duration of the collection period in min. The collection rate, V_f (μl/min), was measured directly from the volume and duration of each collection. All volumes were estimated gravimetrically to 10^{-4} g. The net water flux, J_v (μl.cm^{-2}.h^{-1}), was calculated as:

$$J_v = \frac{(V_0 - V_f)(60)}{A},$$

where A represents the surface area (cm^2) estimated by considering the midgut as a cylinder. The estimated surface area was between 0·4 and 0·75 cm^2. A 6·8 g lobster provided a preparation of approximtaely 0·56 cm^2.

The composition of perfusate and serosal bath was identical except that the perfusate contained [^{14}C]inulin (0·25 μCi/ml) and 0·05% unlabelled inulin to minimize adsorption of radioactivity upon the walls of the tubing. Midgut preparations were perfused for 20–30 min before initiation of sampling. Usually six 5 min collections were obtained from each preparation. Bath samples (1 ml) were taken at the end of the collection period to determine extent of leakage. Preparations with leakages greater than 0·10% of the perfusion rate were eliminated from further consideration. Distilled water (2·5 ml) and 10 ml Aquasol were added to vials containing either 0·5 ml initial perfusate samples, collected perfusate effluent (approximately 0·5 ml), or bath samples (1 ml). The vials were set aside for at least 24 h before counting in a Packard Tri-Carb liquid scintillation spectrometer.

Classification of moult stages was based on that of Drach (1939) and Drach & Tchernigovtzeff (1967). Proecdysis (stage D) subdivisions were as defined by Aiken (1973). For juvenile lobsters raised at 19 °C, moult stages are as follows. Stage D_3'' animals are within 24–36 h of ecdysis. Stage D_4 begins 45–60 min before ecdysis when sea-water uptake commences. At this time the carapace swells and begins to lift. Stage E, or ecdysis, is restricted to exuviation, or the active withdrawal of the animal from the exoskeleton, and lasts 15–20 min.

In postmoult stage A, the cuticle is soft, supple, and easily deformed. Stage A_1' are animals immediately following ecdysis. Uptake of water continues through the duration of this stage (0–2 h postecdysis). Stage A_1'' begins when water ingestion is completed (2 h postecdysis). Final distension of the new cuticle, particularly that of the chelae, occurs during this stage (2–4 h postecdysis). The beginning of stage A_2 is defined as the time at which the cuticle is fully distended. Stage A_2 has been subdivided on the basis of time after ecdysis. Stage A_2' and A_2'' individuals are 4·5 and 8·5 h postecdysis, respectively. Consumption of the shed exuvium begins 12–18 h after ecdysis. Most of the exuvium is consumed by stage B (3–4 days postecdysis); the cuticle has hardened to a parchment-like consistency. The exoskeleton of stage C_4 animals (14–15 days postecdysis) is hard and fully formed.

Table 1. *Osmolality (m-osmol/kg H_2O) of haemolymph during the moulting cycle in juvenile* Homarus americanus*

Moult stage	Osmolality (m-osmol/kg H_2O)
C_4	991·4 ± 0·9 (8)†
D_3	993·7 ± 4·3 (10)
A	980·5 ± 5·6 (6)

* Sea water = 982 m-osmol/kg H_2O.
† Mean ± 1 S.E. (n).

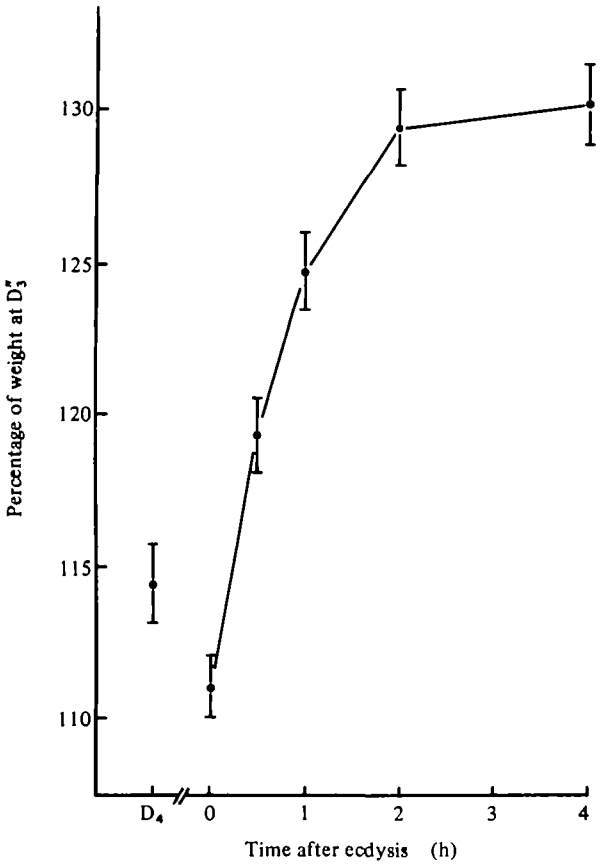


Fig. 1. Whole-animal wet weight of juvenile *Homarus americanus* in late proecdysis (stage D_4) and in the hours immediately following ecdysis expressed as percentage of wet weight at stage D_3'. Mean ± 1 S.E. (n = 10).

RESULTS

Haemolymph osmolality of juvenile *Homarus americanus* remained essentially iso-osmotic to sea water (982 m-osmol/kg H_2O) during the moulting cycle (Table 1). The blood of stages C_4 and D_3 individuals was slightly hyper-osmotic to sea water (991·4 and 993·7 m-osmol/kg H_2O, respectively). Osmolality of stage A animals declined to 980·5 m-osmol/kg H_2O, which was significantly different from the means of the other moult stages ($P < 0.05$).

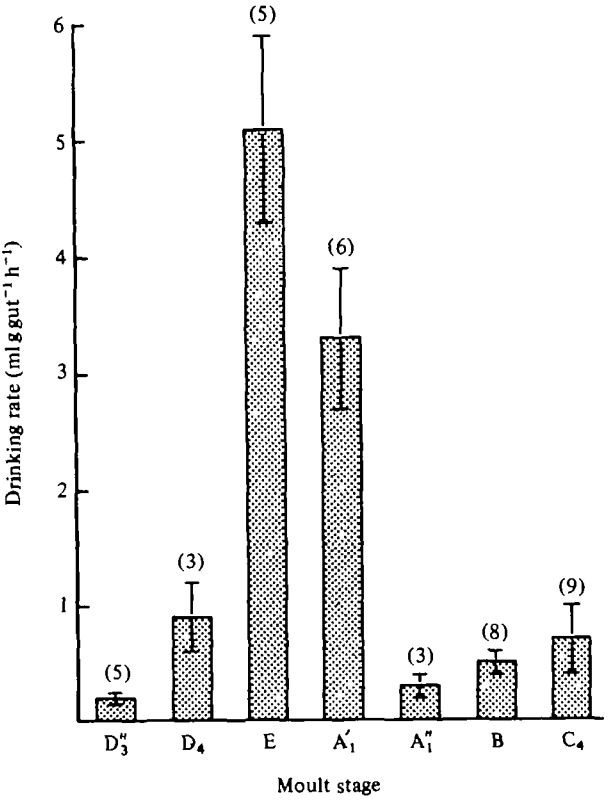


Fig. 2. Drinking rate (ml.g^{-1}.h^{-1}) of juvenile *Homarus americanus* during the moulting cycle; expressed as mean ± 1 S.E. (n). Moult stages defined in Materials and Methods.

A large increase in whole-animal wet weight occurred at moult (Fig. 1), commencing at stage D_4. A transient weight loss accompanied the loss of the exuvium (18% of D_3'' weight). But this was followed by a rapid weight increase in the 2 h following ecdysis. Weight then increased more slowly. By 4 h after ecdysis, lobsters weighed 30·2% more than in late premoult. The total amount of water absorbed at moult (W_3) was equal to 48·2 ± 1·6% of the premoult weight.

The drinking rate of lobsters varied significantly with stage of the moulting cycle and was greatest during the period of weight increase (Fig. 2). Drinking rate can be seen to rise considerably at ecdysis and 0·5 h postecdysis. The mean values for these stages (E and A_1') were significantly greater ($P < 0.01$, Newman–Keuls test of Zivin & Bartko, 1976) than the means of the other groups (stages D_3'', D_4, A_1'', B, and C_4).

Table 2 shows that there is no significant difference between the total quantity of water absorbed and the quantity of water ingested during and immediately following ecdysis.

Both water content and haemolymph volume varied significantly during the moulting cycle (Fig. 3). Water content was lowest at stage D_3'' and rose steadily to maximum values 2·5–8·5 h after ecdysis (stages A_1'', A_2', A_2''). Water content then steadily declined. All group means were significantly different from each other ($P < 0.05$, Newman–

Table 2. *Comparison between the quantity of water absorbed (g) and quantity of sea water ingested (ml) during moult in juvenile* Homarus americanus

Moult stage	Water absorbed (g)	Water ingested (ml)
E*	0·34 ± 0·03 (5)†	0·36 ± 0·03 (5)
A_1'‡	0·37 ± 0·06 (5)	0·35 ± 0·03 (5)

* Mean D_3'' weight = 1·72 g (range: 1·18–1·97 g).
† Mean ± 1 S.E. (*n*).
‡ Mean weight at 0 h postecdysis = 2·25 g (range: 1·52–2·95 g).

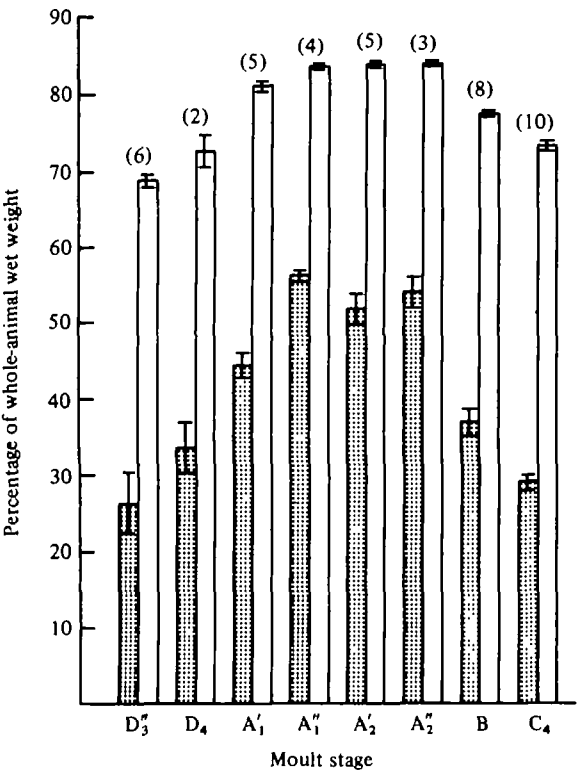


Fig. 3. Total body water (unshaded columns) and haemolymph volume (shaded columns) of juvenile *Homarus americanus*; expressed as percentage ± 1 S.E. (*n*) of whole-animal wet weight, during the moulting cycle. Moult stages defined in Materials and Methods.

Keuls test) except those between stages D_4 and C_4 individuals and between stages A_1'', A_2', and A_2'' animals. Change in haemolymph volume followed a similar pattern. Approximately 91 % of the sea water ingested appeared within the haemolymph by 2·5 h after ecdysis. All group means were significantly different from each other ($P < 0.05$, Newman–Keuls test) except those of stages D_3'', D_4, C_4 stages D_4 and B, and stages A_1'', A_2', and A_2''.

X-radiography of lobsters that had ingested a suspension of barium sulphate during ecdysis demonstrated that the compound entered the midgut within 45–60 min after individuals were placed in the suspension (Fig. 4). Immediately following ecdysis, the

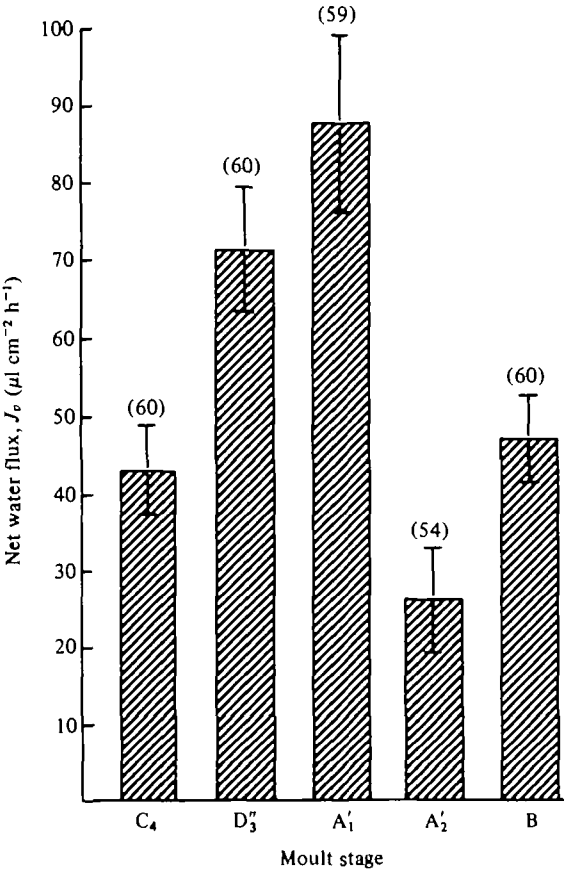
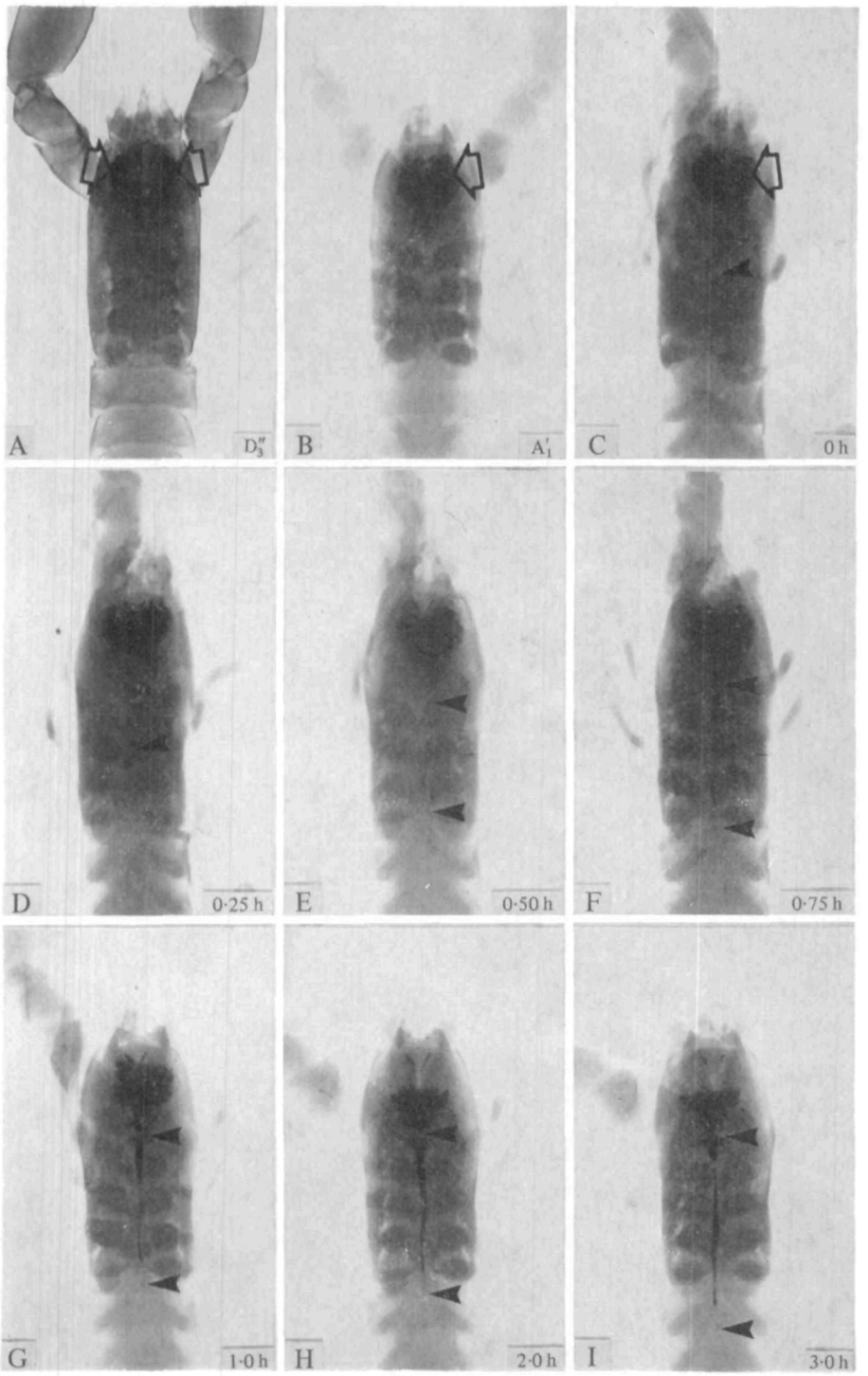


Fig. 5. Net water flux, J_v (μl.cm^{-2}.h^{-1}), across perfused midgut of juvenile *Homarus americanus* during the moulting cycle. Mean ± 1 S.E. (n = number of effluent collections).

proventriculus was filled with gastrolith fragments and barium sulphate. During the first hour after ecdysis, barium sulphate accumulated rapidly in the anterior midgut. There was no apparent accumulation in the hepatopancreas, and gastrolith fragments remained within the proventriculus. By 45 min postecdysis, a well-defined faecal strand had formed. It darkened and became more distinct in the radiographs during the subsequent 1·5 h (1–2·5 h postecdysis). There was no further changes in the opacity of the faecal strand 2·5 and 3 h postecdysis.

Fig. 4. X-radiographs of juvenile *Homarus americanus* (actual size). Animal 1 (A, C–I) was exposed for 65 min to barium sulphate suspension during ecdysis while animal 2 (B) was not exposed to the suspension. (A) Animal 1 in late proecdysis (stage D_3'') before exposure to barium sulphate. Gastroliths (arrows) are fully formed along lateral margins of proventriculus. (B) Animal 2 approximately 1 h after ecysis. Gastrolith fragments fill proventriculus (arrow). (C) Animal 1 immediately following ecdysis and exposure to barium sulphate suspension. Animal has lost its right cheliped during moult. Proventriculus filled with gastrolith fragments and barium sulphate (arrow). A small amount of barium sulphate appears in anterior midgut (arrowhead), which becomes larger and more dense 15 min later (D). At 30 min postecdysis (E), a faecal strand, delineated by arrowheads, has formed. Faecal strand becomes longer and darker 45 min (F), 1 h (G), 2 h (H), and 3 h (I) postecdysis.


A
D$_3''$
B
A$_1'$
C
0 h
D
0·25 h
E
0·50 h
F
0·75 h
G
1·0 h
H
2·0 h
I
3·0 h

Significant alterations in transepithelial net water flux, J_v, were observed in the perfused midgut during the moulting cycle (Fig. 5). The group means of stages D_3'' and A_1' preparations were significantly greater ($P < 0{\cdot}05$, Newman–Keuls test) than those of stages C_4, A_2', and B preparations.

DISCUSSION

The rapid absorption of water at ecdysis in juvenile lobster occurs in the absence of an osmotic gradient between haemolymph and sea water. Water uptake begins about an hour before ecdysis and is completed 2 h after ecdysis. The duration of water uptake is longer in adult *Homarus americanus*, being completed 4–6 h post-ecdysis (Corrivault & Tremblay, 1948). In other decapods, weight gain as a result of water uptake is completed within 4–7 h after ecdysis (Olmsted & Baumberger, 1923; Drilhon, 1935; Drach, 1939; Travis, 1954; Robertson, 1960; Mykles, 1979*a*).

Dall & Smith (1978) have measured large net influxes of tritiated water in the rock lobster, *Panulirus longipes*, during stages D_4 and E, but the surfaces across which the water entered the haemolymph were not determined. The data presented in this investigation provide convincing evidence that the digestive tract of *Homarus* is the sole site of water uptake at moult. The amounts of fluid absorbed and sea water ingested during and immediately following ecdysis are equal. Also, drinking of large quantities of sea water coincides with the weight gain observed. The proventriculus is distended to 2–3 times its normal volume in lobsters immediately following ecdysis (Mykles, 1979*a*).

Haemolymph volume measurements demonstrate that movement of fluid from the gut lumen into the blood space and ingestion of sea water occur simultaneously and are completed by 2·5 h postecdysis. It is estimated that 91% of the sea water ingested appears in the haemolymph by stage A_1''. The data suggest that blood volume expansion may begin before lobsters initiate drinking. Perfused midgut preparations obtained from stage D_3'' animals have elevated net water fluxes, even though intact animals have low drinking rates at this stage. About midway in stage D_4, as lobsters drink sea water, haemolymph volume has already increased about 46% above that of stage D_3'' animals. The large variability of stage D_3'' blood volumes (Fig. 3) suggests that at least some individuals have initiated fluid absorption.

The generation of internal hydrostatic pressure is caused by drinking the medium, which distends the gut (Drach, 1939; Passano, 1960). Hydrostatic pressure is believed essential in loosening and lifting the carapace before exuviation can occur. The extent to which the gut lining can be distended is limited; the absorption of fluid into the haemolymph would allow the animal to ingest greater quantities of sea water, resulting in the generation of greater hydrostatic pressures.

Fig. 6 summarizes the changes in magnitude of the major compartments within a hypothetical 100 g lobster during the moulting cycle. The columns comprising the whole-animal wet weight are divided into three major components; dry weight, extra-haemolymph space, and haemolymph volume. Before ecdysis, dry weight is divided between the exuvium and tissue mass. At moult, 18 g (10·6 g dry weight and 7·4 g water) is lost when the exuvium is shed. Tissue dry weight remains relatively constant

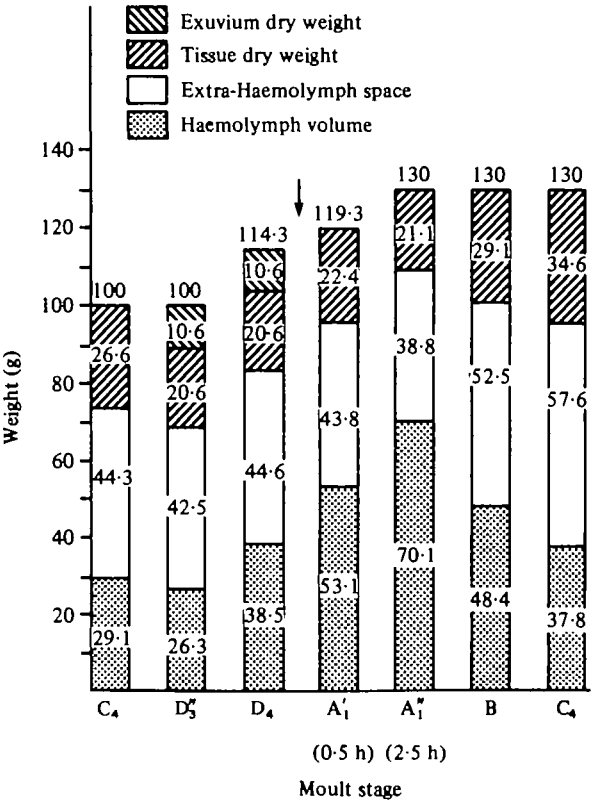


Fig. 6. Partitioning of a hypothetical 100 g lobster into three major tissue compartments during the moulting cycle. This figure summarizes data presented in Figs. 1 and 3. The three compartments comprise haemolymph volume, extra-haemolymph space, and dry weight. Dry weight at stages D_3^* and D_4 partitioned between exuvium and tissue. Numbers within columns are weights (g) of various compartments. Number above each column is total wet weight of hypothetical lobster at each moult stage. Ecdysis occurs at arrow.

through moult (stages D_4, A_1', and A_1^*). In stages B and C_4, dry weight increases because of the combined effects of synthesis and mineralization of the remainder of the cuticle and tissue proliferation (Passano, 1960).

Extra-haemolymph space is the remainder of the body water not contained within the haemolymph and comprises gut fluid, the contents of the antennal gland (urine), intracellular water, and water in the exoskeleton. As haemolymph volume increases from stages D_4 through A_1' and A_1^*, extra-haemolymph space decreases. Because it is improbable that intracellular water, cuticular hydration, or antennal gland volume is changing in such a short interval, the decline in extra-haemolymph space, particularly from stage A_1' to stage A_1^*, may reflect a decrease in gut volume as fluid is absorbed into the haemolymph. Blood volume decreases substantially in the days following ecdysis (stages B and C_4). The reasons appear to be complex. Addition of tissue mass and cuticular materials, as well as the expansion of extra-haemolymph space are responsible. As more cuticle continues to be secreted, more water is invested in the exoskeleton. The gut volume may be larger as digestive enzymes and emulsifiers are secreted upon resumption of feeding by stage B individuals.

The midgut appears to be the principal part of the digestive tract of *Homarus* involved in absorption of ingested sea water into the haemolymph. X-radiography of lobsters that had ingested a barium sulphate suspension at moult (Fig. 4) indicates that formation and consolidation of the faecal strand within the midgut parallels haemolymph expansion during the 2·5 h after ecdysis. Concentration of the compound results presumably from the net absorption of fluid from the lumen. Also correlated with haemolymph expansion, increased net water fluxes across the perfused midgut occur in stages D_3'' and A_1'. Elevated net water fluxes are also observed in the perfused midgut of the freshwater prawn, *Macrobrachium rosenbergii*, during stage D (Mykles & Ahearn, 1978).

Drach (1939) has calculated that a solution similar in composition to sea water is absorbed by the spider crab, *Maia squinado*, at ecdysis. In stenohaline marine decapods, it appears that a fluid iso-osmotic to sea water is transported into the haemolymph because blood solute concentration does not change during the moulting cycle (Lowndes & Panikkar, 1941; Glynn, 1968; Born, 1970; Bursey & Lane, 1971). Both Ahearn *et al.* (1977) and Mykles (1979*a*) have shown that net water transport is linked to solute transport in perfused midgut preparations from *Macrobrachium* and *Homarus*, respectively. The ultrastructural organization of the midgut and midgut caeca of *Homarus* (Mykles, 1979*b*) as well as that of other decapods (Komuor & Yamamoto, 1968; Talbot, Clark & Lawrence, 1972; Mykles, 1977, 1979*b*; Smith, 1978) resembles that of other epithelia capable of active ion transport (Berridge & Oschman, 1972). The basal cytoplasm contains numerous mitochondria and an anastomosing system of smooth endoplasmic reticulum contiguous with the basolateral cell membrane. The ultrastructural and physiological information suggests that solutes, primarily Na^+ and Cl^-, are transported into the lumina of the smooth endoplasmic reticulum, creating a local osmotic gradient that draws water across the apical membrane and leads to an iso-osmotic flow of ions and water across the epithelium and into the haemolymph.

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Note added in proof

Dall and Smith (*J. exp. mar. Biol. Ecol.*, 1978, vol. 35, pp. 165–76) have recently investigated water uptake at ecdysis in the western rock lobster, *Panulirus longipes*. Their findings differ from those presented here in two respects: (1) the quantity of water ingested (13·7% of premoult weight) was less than the total increase in weight (18·4–21·4% premoult weight) at moult and (2) the hepatopancreas, rather than the midgut proper, is the major site of absorption of fluid into the haemolymph. The midgut of *Panulirus* is limited to a short segment where the hepatopancreatic ducts join the digestive tract. Thus, it is probable that the absorptive function has been assumed by one or more cell types in the hepatopancreas of *Panulirus*.