J. exp. Biol. (1977), 70, 221–230
Printed in Great Britain

SALT AND WATER BALANCE OF THE SPINY LOBSTER, *PANULIRUS ARGUS*: THE ROLE OF THE ANTENNAL GLANDS

BY D. F. MALLEY*

Department of Zoology, University of Michigan, Ann Arbor, Michigan 48109, *U.S.A.*

(*Received 22 March* 1977)

SUMMARY

1. *Panulirus argus* in full sea water differs from most other marine isosmotic decapods by regulating Cl^- levels in the haemolymph slightly below those in sea water and by having haemolymph K^+ levels similar to those in sea water. The species is typical in regulating haemolymph Na^+ and Ca^{2+} above, and Mg^{2+} and SO_4^{2-} below, sea-water levels of these ions. Its haemolymph Mg^{2+} and SO_4^{2-} concentrations are amongst the lowest reported in marine decapods.

2. The antennal glands contribute to this regulation of Mg^{2+} SO_4^{2-} and Cl^- by producing urine with markedly, and approximately equally, elevated Mg^{2+} and SO_4^{2-} levels, and slightly elevated Cl^- levels, compared with those in the haemolymph. The antennal glands show a small tendency to conserve water.

INTRODUCTION

Decapod crustaceans are able to regulate total haemolymph osmoconcentration and the concentrations of individual ions at levels different from those in their aquatic environment (Lockwood, 1962, 1967; Potts & Parry, 1963). Further, they actively maintain constant body volume. This clearly is necessary in decapods which are subject to osmotic gain or loss of water, but volume regulation is required even in osmoconformers to replace water lost in urine.

Much attention has been given to the functioning of the gills as sites of active uptake of ions (Koch, 1954; Bielawski, 1964; Lockwood, 1967) and to the antennal glands (Robertson, 1949; Parry, 1955; Gross & Marshall, 1960; Riegel & Lockwood, 1961) in this regulation of salt and water. The antennal glands tend to remove Mg^{2+} and SO_4^{2-} and to conserve K^+ and Ca^{2+} (Potts & Parry, 1963). But fewer studies have been made of the contribution of the gut, the third major interface between the external medium and haemolymph (Green *et al.* 1959; Gifford, 1962; Heeg & Cannone, 1966; Dall, 1967, 1970).

This study was undertaken primarily to examine the possible role of the gut in ionic regulation and water balance of the isosmotic marine lobster, *Panulirus argus* (Latreille).

* Present address: Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba, Canada R3T 2N6.

This paper describes the pattern of ionic regulation demonstrated by this species and the importance of the antennal glands in its maintenance. The following paper (Malley, 1977) reports the ionic analysis of gut fluids, rates of drinking of the medium by lobsters, the movement of water and ions between the proventricular fluid and haemolymph, and assesses the role of the gut in the water and salt economy of this species.

MATERIAL AND METHODS

Maintenance of lobsters

Twenty-three *Panulirus argus* were obtained from two geographical areas, Florida and Bermuda. Fourteen lobsters of both sexes collected off the Florida Keys were air-shipped by a biological supplier to Ann Arbor, Michigan. Carapace length ranged from 6·3 to 8·8 cm at procurance. Lobsters were maintained up to one year at 19 ± 1·5 °C in a continuously circulating closed sea-water system containing a mixture of natural sea water and artificial sea salts (Instant Ocean, Aquarium Systems, Inc., Wickliffe, Ohio) diluted with distilled water. Average composition of this sea water is given in Table 2. Fresh tap-water was added to adjust salinity to between 35 and 37·5‰. Photoperiod was 12 h light, 12 h dark. This set of conditions is referred to as 'laboratory maintenance conditions'. Lobsters were fed pieces of thawed squid, generally two to three times per week. Many lobsters moulted during the maintenance period and nearly all moults were successful.

Nine *Panulirus argus* were obtained directly from the pots of local fishermen in Bermuda and were maintained for 1 week in an open sea-water system at the Bermuda Biological Station under conditions of salinity (35·1‰), temperature (24·0–24·5 °C) and photoperiod (early September) approximating to those in the field. These are referred to as 'field maintenance conditions'. Lobsters were of both sexes and ranged in carapace length from 7·8 to 10·8 cm and in weight from 416·7 to 999·3 g. They were air-shipped to Ann Arbor 1 week after capture and maintained under the 'laboratory maintenance conditions' and fed as described above for over 5 months.

Collection of body fluids

Unless otherwise indicated, all animals had neither recently moulted nor were about to moult when sampled. Lobsters were not fed for at least 2 days prior to sampling.

Before sampling, animals were tied, ventral surface up, to an operating board (see Travis, 1955). Haemolymph was obtained by puncturing the arthrodial membrane proximal to the coxopodite of the fourth or fifth periopod. Serum was obtained following the retraction of the clot in about 1 ml of undiluted haemolymph. Urine was caused to flow by inserting a fine fire-polished glass probe into the nephropore. Samples of the sea-water medium were taken concurrently with body fluid samples. Samples of body fluids and sea water were taken in duplicate or triplicate and were 20 μl in volume, occasionally less, collected and measured in Drummond 'Microcaps' micropipettes. These 20 μl samples were diluted immediately with 2·0 ml distilled water, frozen and stored in air-tight polypropylene tubes until analysed. Samples for SO_4^{2-} analysis, however, were 100 μl of fluids (occasionally only 50 μl was available) diluted with 1·0 ml distilled water.

Analyses

Na^+, K^+, Ca^{2+} and Mg^{2+} were determined in each diluted 20 μl sample by atomic absorption spectrophotometry (Perkin-Elmer Model 290B). Samples for Ca^{2+} analysis were prepared with 0·5% lanthanum oxide to avoid chemical interferences. For K^+ analysis, 100 mM-NaCl was added to overcome ionization interferences.

Chloride was measured in the diluted 20 μl samples with an Aminco-Cotlove chloride titrator using standard techniques. Salinity of sea water was calculated from the chloride concentration using the formula given by Barnes (1954): salinity (‰) = 0·03 + 1·805 × chlorinity ‰. According to the Instant Ocean artificial sea-water formulation, chlorinity is 1·00048 × chloride concentration.

Sulphate was determined as $BaSO_4$ by means of a turbidometric method (American Public Health Association, 1965), modified for microsamples. Absorption was measured at 420 nm.

Osmoconcentration of serum and sea water was measured on a Mechrolab Model 301A vapour pressure osmometer using NaCl solutions as reference standards.

Values from the analysis of the duplicate or triplicate samples of a single fluid were averaged and the mean constitutes a determination.

The data from the ion analyses were in molar concentration. Since the content of water varies in the different fluids, the actual ionic gradients between fluids are seen when ion levels are expressed in molal concentration. To determine the water content of body fluids and sea water, samples of known volume and weight were dried to constant weight at 90–100 °C. Serum was substituted here for haemolymph which clots if it is not immediately diluted with water. There is essentially no osmotic difference between haemolymph and serum in several species of decapods examined (Gross, 1964; see also Table 2, serum as % haemolymph). Ion concentrations were converted from molar to molal by multiplying by conversion factors: 1000 g H_2O/weight in g of water in 1 l of fluid, separately determined for sea water, serum and urine.

Serum (50–1000 μl) was dialysed against the sea water in which the animal was maintained. Dialysis was carried out for 12–24 h at 5 °C in 1 l of sea water on a shaker or with magnetic stirring.

RESULTS

Regulation of ionic concentrations in the haemolymph

The body fluids of nine *Panulirus argus* were sampled at the Bermuda Biological Station within 1–3 days of their capture from the field. Table 1 shows the molar concentrations of Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^- and SO_4^{2-} and the water content in haemolymph and urine of these lobsters and in Bermuda sea water. These values are the closest estimates obtained in this study of body fluid concentrations of *P. argus* under natural conditions. The effective ionic gradients between fluids are indicated by expressing ionic concentrations on a molal basis. The factors for converting the data in Table 1 from molar to molal are for blood, 1·038; urine, 1·016; and sea water, 1·019.

Table 2 shows molal concentrations of the major inorganic ions in haemolymph,

Table 1. *Ionic composition and water content of sea water and body fluids of* Panulirus argus *sampled under 'field maintenance conditions' in Bermuda*

Fluid	Concentrations of ions (mM)						Water content (% wet weight)
	Na^+	K^+	Ca^{2+}	Mg^{2+}	Cl^-	SO_4^{2-}	
Haemolymph	498±6	10·7±0·4	13·5±0·3	11·3±0·8	504±5	17·8±1·6	93·4±0·6
N	8	9	9	9	9	5	(serum 6
Urine	513±6	11·5±0·5	13·7±0·4	16·0±1·4	541±3	19·7±1·4	96·5±0·2
N	8	8	8	8	8	5	9
Sea water	462±2	10·0±0·1	10·5±0·1	53·6±0·3	547±2	28·1±0·2	96·1±0·1
N	17	17	17	17	17	14	10

Values are means ± standard error. *N* = number of determinations from a total of nine lobsters.

Table 2. *Comparisons of molal ionic concentrations between haemolymph, serum, dialysed serum and sea water*

Comparison	Na^+	K^+	Ca^{2+}	Mg^{2+}	Cl^-	SO_4^{2-}
Haemolymph						
(% sea water)	107·3±0·5	102·0±1·7	135·5±1·7	24·5±0·7	93·3±0·5	50·6±4·1
N	56	57	57	57	57	33
P	< 0·01	> 0·2	< 0·01	< 0·01	< 0·01	< 0·01
Dialysed serum						
(% sea water)	102·1±0·8	105·6±2·1	113·8±1·6	106·9±0·8	100·7±0·8	104·1±3·5
N	13	13	13	13	13	8
P	< 0·05	< 0·02	< 0·01	< 0·01	> 0·3	> 0·2
Serum						
(% dialysed serum)	109·5±1·1	100·1±3·0	115·5±2·3	24·2±1·4	97·8±0·8	54·0±10·8
N	13	13	13	13	13	6
P	< 0·01	> 0·5	< 0·01	< 0·01	< 0·02	< 0·01
Serum						
(% haemolymph)	101·1±0·4	101·6±2·0	102·1±0·8	101·1±0·8	101·4±0·3	95·6±2·7
N	14	14	14	14	14	6
P	< 0·02	> 0·4	< 0·02	> 0·1	< 0·01	> 0·1

Average millimolal concentrations in laboratory sea water (*N* = 38; except SO_4^{2-} = 25): Na^+, 476·9; K^+, 10·5; Ca^{2+}, 11·4; Mg^{2+}, 57·1; Cl^-, 564·8; SO_4^{2-}, 28·9.

Values are means ± standard error of *N* percentages. *N* = number of determinations from lobsters sampled under either field or laboratory maintenance conditions.

Data for haemolymph were from 9 Bermuda and 14 Florida lobsters; for serum from 4 Bermuda and 8 Florida lobsters.

P = probability that the mean is equal to 100 using Student's *t*.

serum, dialysed serum and sea water as percentages of one another for 23 lobsters from both Bermuda and Florida. These data include the values given in Table 1 as well as determinations made after lobsters were maintained for varying lengths of time in the laboratory. Ionic concentrations are expressed as ratios to allow pooling of data from animals equilibrated with slightly different salinities. Ionic gradients between haemolymph and sea water reflect both active processes of ion regulation and passive factors such as presence of protein and the binding of Ca^{2+} (Robertson, 1949). Dialysis of serum against sea water shows that passive factors account, in *P. argus*,

Table 3. *Comparisons of molal ionic concentrations between haemolymph, urine and the calculated ultrafiltrate of haemolymph*

Comparison	Na^+	K^+	Ca^{2+}	Mg^{2+}	Cl^-	SO_4^{2-}
Urine (% haemolymph)	101·1 ± 0·4	101·9 ± 3·2	92·8 ± 1·3	132·0 ± 5·5	104·7 ± 0·7	131·7 ± 2·8
N	37	38	38	38	38	24
P	< 0·05	> 0·5	< 0·01	< 0·01	< 0·01	< 0·01
Haemolymph ultrafiltrate* (% haemolymph)	97·9	94·7	87·9	93·6	99·3	96·1
Urine (% haemolymph ultralfiltrate*)	103·3	107·6	105·6	141·0	105·4	137·0

Values are means ± standard error of *N* percentages. *N* = number of determinations from 9 Bermuda and 14 Florida lobsters sampled under either field or laboratory maintenance conditions. *P* = probability that the mean is equal to 100 using Student's *t*.

* Calculated as the reciprocal of 'dialysed serum as % sea water' ratios given in Table 2.

for some elevation of haemolymph Na^+, K^+, Ca^{2+} and Mg^{2+} above sea water levels (Table 2, dialysed serum as % sea water). Measurable amounts of haemolymph Ca^{2+}, Mg^{2+} and K^+ are non-dialysable and thus assumed to be bound. But active ion regulation, seen by comparing serum with dialysed serum, is generally more important than passive factors in accounting for the ionic gradients in this species. Concentrations of Na^+ and Ca^{2+} in haemolymph are actively regulated above those values in passive equilibrium with sea water, to 109 and 116% respectively. Levels of Mg^{2+} (24%), Cl^- (98%) and SO_4^{2-} (54%) in the haemolymph are regulated below sea water concentrations. K^+ concentration in the haemolymph is variable and may be above or below sea-water concentrations. This ion appears not be regulated at levels different from those in sea water.

Total haemolymph osmoconcentration is similar to that of full sea water. Osmoconcentrations of serum from four Bermuda lobsters were 1052, 1115, 1086 and 1037 mosmol/l, averaging 99·6% of the laboratory sea water of mean salinity of 36·6‰.

Role of the antennal glands in the regulation of haemolymph ionic concentrations

Table 3 shows that urinary concentrations of Na^+, Mg^{2+}, Cl^- and SO_4^{2-} exceed those in the haemolymph, whereas Ca^{2+} in the urine is lower than in the haemolymph. Concentrations of K^+ in the two fluids are not statistically different. These results indicate that the antennal glands help to regulate Mg^{2+}, SO_4^{2-} and Cl^- levels in the haemolymph. The antennal glands are not effective in maintaining haemolymph concentrations of Na^+ and Ca^{2+} above those in sea water since they do not conserve these ions. For example, a portion sufficient to raise dialysed serum Ca^{2+} 14% above sea water is bound and unavailable for filtration (Table 2, dialysed serum as % sea water), but urinary Ca^{2+} concentration is only about 7% below haemolymph values. The simplest explanation of urine formation in *P. argus* based on these data (urine as % haemolymph ultrafiltrate) is that the antennal gland forms an ultrafiltrate of the haemolymph from which it resorbs about 5% of the water and into which it secretes Mg^{2+} and SO_4^{2-}.

Table 4. *Results of analysis of covariance performed for five ions on changes with time in haemolymph concentrations* as percentages of sea-water concentration*

Ion	*N*	Time axis	Regression coefficient (covariation removed)	*P*	Mean % change in haemolymph/sea water between days 1 and 165
Na^+	14	Linear	0·025	0·015	+4%
K^+	13	Linear	0·062	0·048	+10·5%
Ca^{2+}	14	Linear	Days 1–22, 0·622†	0·000	Days 1–15, +6·6%
		Linear	Days 9–164, 0·128†	0·001	Days 15–165, −16%
Mg^{2+}	14	Log	2·4	0·002	+28%
Cl^-	14	Linear	0·039	0·000	+7·2%

N is the number of animals. *P* is the probability that the regresssion coefficient is equal to zero. Mean % change among lobsters is calculated from the regression equation of each ion. It is the difference between the day 165 value and the concentration at day 1, expressed as % of day 1 value, except for Ca^{2+}.

* Concentrations of all ions, molal.

† Some Ca^{2+} determinations are included in both regression calculations.

Variations in haemolymph ion levels with time and geographical location

Due to the distance of the laboratory setting from the natural habitat and ready supply of *P. argus* it was necessary to maintain specimens for considerable periods of time under artificial conditions. The haemolymph of the fourteen lobsters obtained from Florida was sampled initially 7–16 days after arrival in the laboratory and then from one to three times thereafter: between 16 and 28 days, at 3 months and/or at $5\frac{1}{2}$ months. The time a lobster was first sampled was termed day 1 for that animal. The ratio of haemolymph to sea-water concentrations for each ion was regressed against time with variation among individuals removed by analysis of covariance. Mean salinity of sea water when lobsters were sampled varied from 35·6 to 36·5‰. Table 4 shows that haemolymph concentrations of Na^+, K^+, Mg^{2+}, Cl^- and initially Ca^{2+} increased significantly with time. Too few SO_4^{2-} determinations were performed on haemolymph for inclusion in this analysis. The 4% rise in concentrations of Na^+ over 5 months is probably of negligible importance. Concentration of Ca^{2+} ion in haemolymph sampled between days 9 and 22 was markedly higher than on day 1. But by 5 months it had decreased to values below those on day 1. The increase in Mg^{2+} concentration in the haemolymph was most rapid initially, then levelled off. The increase was significantly more linear with log time than with arithmetic time according to the *F* test of homogeneity of variance. This ion showed the greatest mean percent change over 5 months. The increase in haemolymph Cl^- concentration was also most rapid during the 2–3 weeks after the first sampling and the rate of change decreased thereafter. The increases in concentrations of Mg^{2+}, Cl^- and the decrease in Ca^{2+} concentrations bring the levels of these ions closer to those in sea water.

The lobsters from Bermuda maintained 13·5 weeks in the laboratory showed the same pattern of ion regulation as did the same individuals sampled in Bermuda within a few days after capture. There were a few statistically significant changes in ion levels after the laboratory maintenance; Mg^{2+} and Cl^- haemolymph levels increased by 11·1% ($P < 0{\cdot}01$) and 3·7% ($P < 0{\cdot}05$), respectively. In another comparison lobsters from Florida maintained 12·5 weeks in the laboratory showed the same pattern of ion regulation as Bermuda lobsters maintained similarly for 13·5 weeks. Florida

lobsters, however, regulated haemolymph Cl^- significantly lower relative to sea water by 2·7% ($P < 0.025$) than did Bermuda animals. These comparisons are presented in Malley (1972).

DISCUSSION

Regulation of ionic concentrations in the haemolymph

Panulirus argus is isosmotic with sea water but shows pronounced regulation of Na^+, Ca^{2+}, Mg^{2+}, SO_4^{2-} and Cl^- in the haemolymph at levels different from those in sea water. Most marine decapods are isosmotic with their environment and regulate Na^+, K^+ and Ca^{2+} above, and Mg^{2+} and SO_4^{2-} below, sea-water values. Chloride is generally in passive equilibrium between haemolymph and sea water (Robertson, 1960). *Panulirus argus* thus differs from the majority of marine decapods in regulating haemolymph Cl^- levels and in not regulating those of K^+. Otherwise this species is typical in its isosmoticity with sea water and its regulation of Na^+, Ca^{2+}, Mg^{2+} and SO_4^{2-}.

Osmotic and ionic regulation has been documented in the tropical rock lobster *Panulirus longipes* in a study by Dall (1974) published after the present study was completed. In *P. longipes* in ambient sea water of 36‰, molar concentrations of ions in the haemolymph as functions of molar concentrations in the sea water were Na^+, 106·8%; K^+, 104·1%; Ca^{2+}, 122·7%, Mg^{2+}, 22·8% and Cl^-, 91·4%. Sulphate was not measured. Thus *P. longipes* shows precisely the same pattern of ionic regulation as *P. argus*, also maintaining haemolymph Cl^- below sea water levels ($P < 0.001$) and not maintaining haemolymph K^+ different from full sea water concentration (N.S.). Interestingly, *P. longipes* does regulate K^+ in other salinities, at supra sea-water concentrations when the lobster is in lower salinities down to 20‰ and at sub sea-water concentrations when immersed in higher salinities up to 45‰. Ion concentrations in the serum of the related *Palinurus elephas* are similar to the haemolymph levels reported here for *P. argus* except that *P. elephas* does not regulate Cl^- (Robertson, 1949).

Panulirus argus has haemolymph Mg^{2+} and SO_4^{2-} levels, relative to sea water, amongst the lowest in marine decapods (Robertson, 1953; Prosser, 1973) although relatively lower Mg^{2+} values have been reported in Homaridae (Robertson, 1949) and marine pandalid shrimp (Mackay & Prosser, 1970). A number of species which can invade brackish water (Parry, 1955) and fresh water (Prosser, 1973) also have low haemolymph Mg^{2+} levels. Low Mg^{2+} levels are correlated in the palinurids, as in the related homarids, with a relatively high level of activity. Magnesium ion is noted for its anaesthetic effect (Heilbrunn, 1952). The tendency for low haemolymph Mg^{2+} levels to be accompanied by slightly raised Na^+ levels (Robertson, 1949) can be seen in *P. argus* as well.

The proportionately large changes in concentrations of Ca^{2+} and Mg^{2+} in the haemolymph which occur with time may indicate that significant changes in some aspects of ion metabolism occur during the time that animals are commonly maintained in the laboratory. Nevertheless, although the magnitude of the ionic gradients between haemolymph and sea water decreases for Ca^{2+}, Mg^{2+} and Cl^-, these ions continue to be regulated. The species of ions regulated in the haemolymph and the

role of the antennal gland in this regulation remain constant between the Florida and Bermuda populations of this species, when lobsters are transferred from field to laboratory maintenance conditions and when they are maintained in the laboratory for up to 5 months. In this study data from the two geographically separated populations have been pooled.

Role of the antennal glands

Panulirus argus demonstrates little conservation of water, resorbing only an estimated 5% of the volume of the untrafiltrate. Burger (1957) found that the marine lobster *Homarus americanus* also shows little or no tendency to resorb water from the urine as evidenced by urine/haemolymph (U/H) inulin ratios of 1·0–1·1. In contrast, the shore crab *Carcinus maenas* in 100% sea water absorbs considerable water from the urine resulting in U/H inulin ratios of about 2·0 (Riegel & Lockwood, 1961). Water conservation in *C. maenas* is presumably an adaptation to littoral life. Exposure of the latter species to water-saturated air for 4 days results in enhanced water resorption from the urine with U/H inulin values rising to 2·4 (Riegel & Lockwood, 1961). The small degree of water resorption from the urine by *P. argus* correlates with its being marine and strictly non-intertidal, like *H. americanus*, and relatively stenohaline.

The antennal glands of *P. argus* are effective in the hyporegulation of Mg^{2+}, SO_4^{2-} and Cl^- in the haemolymph. Although the haemolymph levels of Mg^{2+} and SO_4^{2-} are among the lowest reported in decapod crustaceans, the antennal gland does not concentrate these ions to the extent seen in certain other decapods. In the spiny lobster, Mg^{2+} and SO_4^{2-} U/H values are 1·3 (Table 3). This contrasts with U/H values reported for Mg^{2+} in *Carcinus maenas* in 100% sea water of about 4 (Riegel & Lockwood, 1961) or about 8 (Lockwood & Riegel, 1969). These authors do not report results for SO_4^{2-}. Elevation of Mg^{2+} in the urine of *C. maenas* is in part associated with the resorption of water from the presumptive urine. Sodium, K^+, Ca^{2+} and possibly Cl^- are also resorbed (Riegel & Lockwood, 1961). Magnesium is therefore passively concentrated in the urine. In addition, Mg^{2+} is secreted into the urine and this is paralleled by a withdrawal of Na^+ from the urine against a concentration gradient. For Na^+, U/H values in 100% sea water are about 0·75 (Lockwood & Riegel, 1969). Reciprocal urinary Mg^{2+} and Na^+ concentrations are observed as well in the lined shore crab, *Pachygrapsus crassipes* (Gross & Capen, 1966). The exchange between Na^+ and Mg^{2+} is apparently not 1:1. In contrast to these results, in *P. argus* elevated urinary Mg^{2+} concentrations are not associated with reduced Na^+, and U/H of Na^+ is close to 1·0. *Panulirus argus* concentrates urinary SO_4^{2-} to the same extent as Mg^{2+} and would appear to maintain electrical balance in this way, rather than by exchanging Mg^{2+} for Na^+.

Handling of SO_4^{2-} by the antennal gland has been less thoroughly studied than for Mg^{2+}. Antennal glands of *Carcinus maenas* concentrate SO_4^{2-} to 224% of haemolymph values (Webb, 1940); of the spider crab *Maia squinado* to 214% (Robertson, 1953); of the crab *Cancer pagurus* to 133% (Robertson, 1939); and of the lobster *Homarus vulgaris* to 159% (Robertson, 1949). The lobster *Nephrops norvegicus* concentrates only to 106% and *Palinurus vulgaris* not at all (Robertson, 1949). As for Mg^{2+}, *P. argus* maintains haemolymph SO_4^{2-} low relative to sea water, about 50% compared with 60% in *C. maenas* (Webb, 1940). But the antennal glands of the spiny lobster do

not concentrate this ion to the extent that *C. maenas* does and U/H is 1·3 in the lobster compared with the 2·2 in the crab as mentioned above.

The concentration of Cl^- by the antennal gland is modest (U/H, 1·05), in keeping with the small hyporegulation of the haemolymph Cl^- (serum as % dialysed serum, 98%).

In summary, *Panulirus argus* shows little tendency to conserve water by resorption from the urine. There appears to be little tendency after ultra-filtration for ions to exchange between haemolymph and the presumptive urine except for Mg^{2+} and SO_4^{2-} which appear to be secreted into the urine and in more or less equal quantities. The data suggest that the Mg^{2+} secreted into the urine is not exchanged for Na^+, or at least not to the extent seen in several species of shore crabs. Urinary concentrations of Mg^{2+}, SO_4^{2-} and Cl^- exceed those in the haemolymph, indicating a role of the antennal glands in the regulation of these ions.

This paper is based on a dissertation submitted to the Department of Zoology, University of Michigan, in partial fulfilment of the requirements for the Ph.D. degree. The research at the Bermuda Biological Station for Research, St George's West, Bermuda, was supported by a Horace H. Rackham Dissertation Grant. I wish to thank the director and staff of the Bermuda Biological Station for assistance in obtaining lobsters. My thanks to Dr. Wong Tat Meng of the University of Science of Malaysia and Prof. R. Freeman of the University of Otago, New Zealand, for valuable suggestions on an early stage of the manuscript.

REFERENCES

AMERICAN PUBLIC HEALTH ASSOCIATION (1965). *Standard Methods for the Examination of Water and Wastewater, including Bottom Sediments and Sludges.* New York.

BARNES, H. (1954). Some tables for the ionic composition of sea water. *J. exp. Biol.* **31**, 582–88.

BIELAWSKI, J. (1964). Chloride transport and water intake into isolated gills of crayfish. *Comp. Biochem. Physiol.* **13**, 423–32.

BURGER, J. W. (1957). The general form of excretion in the lobster *Homarus*. *Biol. Bull. mar. biol. Lab., Woods Hole* **113**, 207–23.

DALL, W. (1967). Hypo-osmoregulation in Crustacea. *Comp. Biochem. Physiol.* **21**, 653–78.

DALL, W. (1970). Osmoregulation in the lobster, *Homarus americanus*. *J. Fish. Res. Bd Can.* **27**, 1123–30.

DALL, W. (1974). Osmotic and ionic regulation in the western rock lobster *Panulirus longipes* (Milne-Edwards). *J. exp. mar. Biol. Ecol.* **15**, 97–125.

GIFFORD, C. A. (1962). Some aspects of osmotic and ionic regulation in the blue crab, *Callinectes sapidus*, and the ghost crab, *Ocypode albicans*. *Publs Inst. mar. Sci. Univ. Tex.* **8**, 97–125.

GREEN, J. W., HARSCH, M., BARR, L. & PROSSER, C. L. (1959). The regulation of water and salt by the fiddler crabs, *Uca pugnax* and *Uca pugilator*. *Biol. Bull. mar. biol. Lab., Woods Hole* **116**, 76–87.

GROSS, W. J. (1964). Water balance in anomuran land crabs in a dry atoll. *Biol. Bull. mar. biol. Lab., Woods Hole* **126**, 54–68.

GROSS, W. J. & CAPEN, R. L. (1966). Some functions of the urinary bladder in a crab. *Biol. Bull. mar. biol. Lab., Woods Hole* **131**, 272–91.

GROSS, W. J. & MARSHALL, L. A. (1960). The influence of salinity on the water fluxes of a crab. *Biol. Bull. mar. biol. Lab., Woods Hole* **119**, 440–53.

HEEG, J. & CANNONE, A. J. (1966). Osmoregulation by means of a hitherto unsuspected osmoregulatory organ in two grapsoid crabs. *Zool. Afri.* **2**, 127–9.

HEILBRUNN, L. V. (1952). *An outline of General Physiology*, 3rd ed. London: Saunders.

KOCH, H. J. (1954). Cholinesterases and active transport of sodium chloride through the isolated gills of the crab *Eriocheir sinensis*. In *Recent Developments in Cell Physiology* (ed. J. O. Kitching), pp. 15–27. London: Butterworth.

LOCKWOOD, A. P. M. (1962). The osmoregulation of Crustacea. *Biol. Rev.* **37**, 257–305.

LOCKWOOD, A. P. M. (1967). *Aspects of the Physiology of Crustacea.* San Francisco: W. H. Freeman.

LOCKWOOD, A. P. M. & RIEGEL, J. A. (1969). The excretion of magnesium by *Carcinus maenas*. *J. exp. Biol.* **51**, 575–89.

MACKAY, W. C. & PROSSER, C. L. (1970). Ionic and osmotic regulation in the king crab and two other North Pacific crustaceans. *Comp. Biochem. Physiol.* **34**, 273–80.

MALLEY, D. F. (1972). Role of the gut in salt and water balance of the spiny lobster, *Panulirus argus*. Ph.D. thesis, University of Michigan.

MALLEY, D. F. (1977). Salt and water balance of the spiny lobster *Panulirus argus*: the role of the gut. *J. exp. Biol.* **70**, 231–245.

PARRY, G. (1955). Urine production by the antennal glands of *Palaemonetes varians*. (Leach). *J. exp. Biol.* **32**, 408–22.

POTTS, W. T. W. & PARRY, G. (1963). *Osmotic and Ionic Regulation in Animals*. New York: Pergamon Press.

PROSSER, C. L. (1973). *Comparative Animal Physiology*, 3rd ed. Philadelphia, London: W. B. Saunders.

RIEGEL, J. A. & LOCKWOOD, A. P. M. (1961). The role of the antennal gland in the osmotic and ionic regulation of *Carcinus maenas*. *J. exp. Biol.* **38**, 491–9.

ROBERTSON, J. D. (1939). The inorganic composition of the body fluids of three marine invertebrates. *J. exp. Biol.* **16**, 387–97.

ROBERSTON, J. D. (1949). Ionic regulation in some marine invertebrates. *J. exp. Biol.* **26**, 182–200.

ROBERTSON, J. D. (1953). Further studies of ionic regulation in marine invertebrates. *J. exp. Biol.* **30**, 277–95.

ROBERTSON, J. D. (1960). Osmotic and ionic regulation. In *The Physiology of Crustacea*, vol. 1 (ed. T. H. Waterman), pp. 317–39. London, New York: Academic Press.

TRAVIS, D. F. (1955). The molting cycle of the spiny lobster, *Panulirus argus* Latreille. III. Physiological changes which occur in the blood and urine during the normal molting cycle. *Biol. Bull. mar. biol. Lab., Woods Hole* **109**, 484–503.

WEBB, D. A. (1940). Ionic regulation in *Carcinus maenas*. *Proc. R. Soc. Lond.* B **129**, 107–36.