TEMPERATURE TOLERANCES AND OSMOREGULATION IN SOME ESTUARINE BIVALVES

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ABSTRACT

The salinity and temperature tolerances of some burrowing bivalves which occur in the middle reaches of the Swartkops estuary have been studied. Five species (*Solen capensis, S. corneus, Dosinia hepatica, Macoma litoralis* and *Psammotellina capensis*) have upper lethal temperatures of 41–46°C when heated at a rate of 1 C°/10 minutes. Two species have upper lethal temperatures of 37°C and 39°C when heated at a rate of 1 C°/day. It has been concluded that they can tolerate much higher temperatures than they normally encounter in the estuary.

The salinity tolerances of four species (*S. capensis, S. corneus, Dosinia, Macoma*) have been investigated. All four appear to be euryhaline osmoconformers and can tolerate a wider range of salinities than they normally encounter in nature. Most of them are, however, unable to survive very low salinities, such as occur during floods, for long periods. It has been noted that species with a large gape to their valves come rapidly into osmotic equilibrium with the external medium, while those with no gape can remain closed, and thus survive low salinities for long periods. A strong shell with little gape also has a noticeable insulating effect when the animals are rapidly heated.

INTRODUCTION

Although bivalves are not abundant in South African estuaries (Day 1951), fair-sized populations occur in the middle reaches of the Swartkops estuary, near Port Elizabeth. These bivalve populations, apparently almost unique in South Africa, have provided a good opportunity for comparing the ecology and biology of South African and northern hemisphere estuarine bivalves. This paper covers part of an M.Sc. thesis concerning these bivalves that was submitted to the University of Port Elizabeth by the first author. The rest of the thesis will be published as two further articles in this journal.

Both temperature and salinity can be important environmental factors in estuaries and can influence the distribution of estuarine animals (Day 1951). The Swartkops estuary has a mild climate, and an annual temperature range of 12–28°C has been recorded in the open waters of the parts of the estuary where the bivalves occur. In shallow pools heated at low tide, however, Macnae (1957) has recorded temperatures as high as 36°C. As the temperature thus never drops very low in the estuary and because frost is uncommon, only the upper temperature tolerances of these animals have been studied.

Along most of the estuary the salinity normally remains close to that of seawater (35°/₀₀) and only during very dry conditions or after substantial rains may the estuarine waters become hypersaline (up to about 40°/₀₀) or hyposaline (down to 0°/₀₀). During periodic floods, which characteristically occur every few years (Macnae 1957), the surface waters of practically the whole estuary are fresh (0–2°/₀₀). During such conditions they can remain fresh for at least five days. The normal salinity range to which these bivalves are exposed is 15–37°/₀₀ with a mean of 32°/₀₀, although they are occasionally exposed to practically fresh overlying water for a few days following floods. During floods, salinities within the substrate would, however, tend to remain higher (Duff & Teal 1965, Johnson 1965).

The primary aim of this work was to determine the tolerance limits of some common bivalves to high temperatures and to low and high salinities. The osmoregulatory patterns of the various species were also investigated.

MATERIALS AND METHODS

For all of the experiments described below bivalves were collected intertidally from the middle reaches of the estuary (between the Swartkops brickworks and Redhouse Village) during March, April and May, 1972. The water temperatures recorded here during the day varied between 15,8°C and 24,8°C over this period, while the salinities varied only between 30,9‰ and 36,9‰. Specimens were removed from the substrate by a sieve of 5 mm mesh.

In both the long and short term experiments the following temperatures were noted for each species:

(i) the temperature at which normal activity ceased, i.e. cessation of normal siphonal and foot movements or sluggish response to touching of the siphons or foot.

(ii) the temperature at which heat coma started, i.e. the temperature at which animals began to display no response if their feet or siphons were touched, but recovered on return to room temperature.

(iii) the death point, being the temperature at which 50% of the animals had died or failed to recover after return to a temperature of 20°C.

It was often difficult to observe the exact temperature point at which activity ceased in *Dosinia* as some animals remained closed, and some values were therefore only approximate. In all species the temperature at which coma or death occurred could be determined to within 1 C°. The following experiments were carried out:

1. Long-term temperature tolerance experiment

The aim of this experiment was to study the tolerances of these bivalves to gradually increasing temperatures. Twenty-five specimens of *Dosinia hepatica* (Lamy) and 25 specimens of *Macoma litoralis* (Krauss) were placed into each of two 2 ℓ glass beakers which contained 1 ℓ of sea-water collected from the surf near the Swartkops river mouth. The beakers rested in a waterbath at 22°C. After two days five specimens of each species were left in each beaker and the rest placed in similar beakers at 24°C. The experiment continued in this manner, going in 2 C° steps every 48 hours, until there were duplicate sets of five animals of each species at each of the following temperatures: 22°C, 24°C, 26°C, 28°C and 30°C. From this point onwards the temperatures of all water baths, except the control at 22°C, were raised by 2 C° every second day, until the first bath reached 38°C. The experiment then continued only at 22°C (control), 36°C and 38°C, the remainder being removed. When the first bath had reached 40°C, and all the animals in it were dead, the experiment was terminated.

During the period of this experiment all beakers were checked at least once a day, when distilled water was added to compensate for evaporation and dead animals were counted and removed. Whenever animals had died, fresh sea-water, first heated to the required temperature, was used to replace the old water. Temperatures were regularly checked with a thermometer accurate to 0,1 C° and varied less than 0,5 C° from the values stated. Above 30°C all beakers were aerated. The total duration of the experiment was 20 days.

2. *Short term temperature tolerance experiment*

The aim of this experiment was to study the tolerances of some common bivalves to rapidly increasing temperatures, such as may be experienced during low tide when the intertidal banks are heated by the sun. Into each of two 2 ℓ glass beakers containing 1 ℓ of fresh sea-water were placed 10 *Dosinia hepatica*, 10 *Macoma litoralis*, 10 *Solen corneus* Lamy, eight *S. capensis* Fischer and five *Psammotellina capensis* Sowerby. The difficulty in obtaining specimens necessitated using the above numbers of the different species. Each beaker was aerated and floated in a 5 ℓ beaker containing approximately 2 ℓ of tap-water. This larger beaker was heated by a bunsen burner. Both beakers started at 20°C and were heated at a rate of 1 C° every 10 minutes. A temperature probe, resting on the bottom of each beaker amongst the animals, accurately recorded the temperatures. This was also checked with a thermometer accurate to 0,1 C°. At every degree Celsius above the temperature at which a species showed no response to being touched, a specimen was removed from the beaker concerned and replaced in sea-water at 20°C to see if it recovered.

3. *Size effects experiment*

The aim of this experiment was to quantify any possible insulating effects of the shell valves when bivalves were rapidly heated. This was done during October 1972. A number of specimens were measured to the nearest mm with sliding calipers. (In all cases the length, i.e. the longest antero-posterior diameter of the shell, was measured.) By means of a high-speed electric drill with a 5/64 inch bit, a fine hole was drilled through the mid-ventral margin of one valve of each animal. Some specimens died before or during the experiment and were discarded. A fine iron-constantan thermocouple was inserted into each hole so that the tip came to lie in the mantle cavity of the animal and the hole was then sealed with a fast-setting waterproof glue. The animals were heated as in the short term experiment described above, starting at 20°C (room temperature). The temperatures of the fluids inside the mantle cavities of the bivalves studied, measured by the thermocouples, were read every 10 minutes from a "Transkomp 288 12-channel recorder", accurate to 0,1°C. This had been calibrated with a thermometer accurate to 0,1 C°. This rate of heating (1 C°/10 minutes) was continued until the water reached a temperature of 40,0°C. A temperature of 40°C was then maintained and the time that each specimen took to equilibrate with this temperature measured. This procedure was then repeated during a second run on another group of bivalves. Altogether five *Dosinia*, four *Macoma* and four *Solen corneus* were tested in this way.

4. *Osmoregulation and salinity tolerances of* Solen *spp.*

All animals collected for osmoregulation experiments were kept in sea-water (35‰) for six to eight hours before the commencement of experiments. The first experiment on *Solen* spp.

was done in two parts. In the first part four *S. corneus* and two *S. capensis* were placed into each of seven duplicate pairs of glass dishes containing 500–750 ml of water of the following salinities: 35‰, 28‰, 21‰, 14‰, 10,5‰, 7‰, 3,5‰. In the second experiment five *S. corneus* and two *S. capensis* were placed into similar vessels at the following salinities: 12‰, 25‰, 35‰, 40‰, 45‰. The number of specimens used for each species was dependent on the available supply. These two experiments were done within two weeks of each other. After 24 hours and again after 48 hours those alive were counted and samples of the dish-water and the animal's body fluids were taken from each dish. The criterion for death, as in the temperature tolerance experiments, was gaping of the valves together with the inability of the animals to respond to touching of their feet or siphons. Body fluid was taken from the foot by syringe. The concentrations of 2 ml of the water and body fluids were measured by means of an "Advanced 617 DEcatur 2-8200" freezing-point osmometer, accurate to 1 mOsm. In a few cases where less than 2 ml body fluid could be obtained the accuracy of this method was only ± 2 mOsm. Each value obtained for body fluid concentration was thus based on a mixture of the blood of two or more specimens in the case of *S. corneus* and one specimen in the case of *S. capensis*. As the valves of these animals tend to burst apart without the support of a burrow, and because they rapidly attain osmotic equilibrium with the environment, no experiments longer than two days were performed with them. In the above-mentioned experiments, water lost by evaporation was replaced by distilled water and whenever individuals died, the others in the same dish were changed to a fresh solution.

5. *Osmoregulation and salinity tolerances in* Dosinia hepatica *and* Macoma litoralis

These two species were studied together in an experiment consisting of two parts. In the first part six *Dosinia hepatica* and eight *Macoma litoralis* were placed into each of six duplicate pairs of glass dishes containing approximately 500 ml of water of the following salinities: 35‰, 21‰, 14‰, 7‰, 3,5‰, 0‰. This experiment was terminated after 23 days when the following analyses were carried out on each dish:

(*a*) the dish-water was sampled by syringe and its concentration measured on the freezing-point osmometer as above.

(*b*) mantle-cavity fluid was removed by syringe from those specimens of each species which were still alive in each dish and its concentration determined in a similar manner.

(*c*) some of the mantle-cavity fluid of each species was also collected in a capillary tube and its pH immediately measured on a "Radiometer Copenhagen Acid-base Analyser pHM71".

(*d*) As both species of *Solen* (and in fact most bivalves) are osmoconformers, and preliminary experiments indicated that *Dosinia* and *Macoma* were also osmoconformers, it was considered permissible to use the mantle-cavity fluid as indicative of body fluid. This was done because mantle-cavity fluid is much more easily obtainable than body fluid.

Each value obtained for mantle-cavity fluid was based on a mixture of the fluids of more than one animal, two to four specimens in different cases. The mean was then calculated for the duplicates and this value used.

In the second part of this experiment, carried out a month after the first, eight *Dosinia hepatica* and four *Macoma litoralis* were placed into each of six duplicate pairs of glass dishes at the following concentrations: 0‰, 7‰, 10,5‰, 21‰, 35‰, 45,5‰. The numbers of specimens used here were again dependant on the available supply. After two, five and 11 days, the same determinations were done as in the first part, except that pH values were not measured. In the case of *Macoma litoralis* this was not done after 11 days as there were not sufficient specimens. A minimum of two animals were used for all *Dosinia hepatica* readings and all except a few of the fifth-day readings of *Macoma litoralis*.

In all the above experiments water was prepared by either diluting sea-water (35°/₀₀ = 1 070 mOsm) by addition of glass-distilled water or by concentrating it by evaporation without heating. All vessels took on the normal daily laboratory temperature fluctuations of 18–22°C as well as the normal daily photoperiod. None of the solutions used for salinity tolerance experiments was aerated as preliminary experiments indicated that this was unnecessary.

RESULTS

1. Temperature tolerance experiments

The results of the long and short term temperature tolerance experiments have been summarized in Table 1.

TABLE 1

THE TEMPERATURES AT WHICH NORMAL ACTIVITY CEASES, HEAT COMA STARTS AND DEATH OCCURS AT DIFFERENT RATES OF HEATING IN SIX ESTUARINE SPECIES OF BIVALVES. ALL VALUES IN C°.

	SLOW HEATING (1 C°/day)				*FAST HEATING (1 C°/10 minutes)*			
	Nos. used	*Cessation of activity °C*	*Start of heat coma °C*	*Death point °C*	*Nos. used*	*Cessation of activity °C*	*Start of heat coma °C*	*Death point °C*
Dosinia	50	37	38	39	20	38,5	43,5	45,5
Macoma	50	35	36	37	20	37,5	40	44
S. corneus	—	—	—	—	20	40,5	41	44,5
S. capensis	—	—	—	—	16	40,5	41	41
Psammotellina	—	—	—	—	10	38	39,5	42

In many cases the reactions of different individuals of a species varied slightly. This variation will be discussed when the results of the size-effects experiment, shown in Table 2, are examined. In Table 1 only the mean values are stated.

It is evident from Table 2 that large specimens of *Dosinia hepatica* are better insulated (difference greater) than smaller specimens, while such an effect was not noticeable in the cases of

TABLE 2

THE DIFFERENCES BETWEEN INTERNAL AND EXTERNAL TEMPERATURES IN FOUR SPECIES OF BIVALVES HEATED FROM 20°C TO 40°C AT A RATE OF 1 C°/10 MINUTES. ALSO SHOWN IS THE TIME THE INTERNAL TEMPERATURES TOOK TO EQUILIBRATE TO THE WATER TEMPERATURE WHEN HEATING STOPPED AT 40°C. ALL TEMPERATURES IN C°. THE RESULTS FOR DIFFERENT SIZE-GROUPS OF EACH SPECIES ARE SHOWN SEPARATELY AND THESE RESULTS REPRESENT THE VALUES OBTAINED FROM A LINE PLOTTED USING ALL OF THE POINTS FOR EACH SIZE-GROUP OF EACH SPECIES.

Species	*Nos.*	*Sizes (mm)*	*Internal temperature at 40°C*	*Difference (external — internal)*	*Equilization time at 40°C (minutes)*
Dosinia	2	21; 21	37,8	2,2	25
Dosinia	1	16	38,2	1,8	17
Dosinia	2	13; 12	38,6	1,4	10
Macoma	3	21; 21; 20	39,0	1,0	10
Macoma	1	13	39,0	1,0	10
S. corneus	2	82; 77	38,7	1,3	12
S. corneus	2	47; 41	38,9	1,1	12

Macoma litoralis, or *Solen corneus*. Furthermore *Dosinia* was better insulated (i.e. had a greater lag) than *Solen* which in turn was better insulated than *Macoma*. Possible effects of this insulation and lethal temperatures will be mentioned in the discussion.

2. *Salinity tolerance and osmoregulation experiments*

The results of the osmoregulation experiments on the two species of *Solen* are shown in Figures 1 and 2. From these two figures it can be seen that after 24 hours no specimens of either species survived in salinities below about 8‰ (250 mOsm) and that after 48 hours none survived below 13‰ (400 mOsm). Further, both species survived in salinities at least as high as 42‰ (1 250 mOsm). It can also be seen that both species are osmoconformers and their body fluids equilibrate to the osmotic concentration of the water within 24 hours.

The results of experiments on *Dosinia* and *Macoma* are illustrated in Figures 3 and 4. These two figures show the changes in mantle-cavity fluid concentrations in the two species after different periods of time in different salinities. From this it can be seen that *Macoma*'s mantle-cavity fluid equalizesrapidly with the external medium. In the case of *Dosinia*, however, equalization below the tolerated minimum of about 450 mOsm proceeds very slowly due to tight valve closure. Because of the assumed osmoconformity between the blood and mantle-cavity fluids in both species, the mantle-cavity fluid (which was much more easily obtained) was used as being representative of the body fluid. Thus, in Figures 3 and 4, the concentrations of the mantle-cavity fluids have been plotted against the concentrations of the media. The pH values recorded during these experiments are given in Table 3.

TABLE 3

THE pH VALUES OF THE DISH-WATER AND THE MANTLE-CAVITY FLUIDS OF *Dosinia hepatica* AND *Macoma litoralis* AFTER 23 DAYS IN WATERS OF DIFFERENT SALINITIES.

	WATER		*DOSINIA*		*MACOMA*	
Water salinity ($^0/_{00}$)	*No. samples*	*pH*	*No. specimens*	*pH*	*No. specimens*	*pH*
0	2	8,0	4	7,0	—	—
4,2	1	7,9	4	7,0	—	—
7,7	2	7,7–7,8	4	7,0	2	7,3–7,5
13,8	2	7,5	4	7,0–7,1	2	7,0–7,2
25,0	2	7,8–7,9	4	7,0–7,1	—	—
40,0	2	7,8	4	7,0–7,1	—	—

DISCUSSION

Temperature Tolerances

Henderson (1929) investigated the upper temperature tolerances of 18 marine and estuarine Canadian species of bivalves by heating them at a rate of 1 C° every five minutes. He found that the species studied had lethal temperatures ranging between 31,5°C and 48,0°C and that there was a relationship between the environment in which a species occurred and its upper lethal temperature. The rate of heating is, however, an important factor and Read and Cumming (1967), have used a rate as slow as 1 C° every 3,5 days. Experiments using slow heating indicate the upper temperatures at which a species can live, while those using fast rates of heating indicate the maximum temperatures which these animals can withstand for short periods (Evans 1948) such as might occur during low tide when they are heated by the sun. In slow heating experiments the animals might be able to adapt to some extent, while in fast heating insulation may be important.

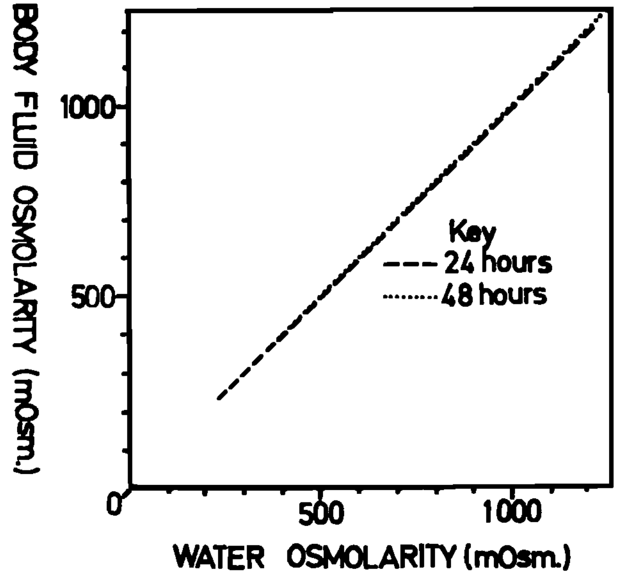

FIGURE 1

Body fluid concentration vs. concentration of the medium in *Solen corneus* after 24 and 48 hours immersion in a range of salinities. All animals acclimated to sea-water (1 070 mOsm). Regression lines:

24 hours: Y = 4,47 + 0,998X. S.D. = ± 0,018
48 hours: Y = 4,29 + 1,007X. S.D. = ± 0,257

The bivalves studied here, when heated rapidly, conform to the pattern found by Henderson (1929). They all come from the same environment (intertidal muds of the middle reaches of the Swartkops estuary) and all have upper lethal temperatures in the narrow range of 41–46°C, when heated at 1 C° per 10 minutes. Furthermore, their lethal temperatures fall in the upper part of the range recorded by Henderson (1929). As they are all intertidal forms that are exposed to a reasonable amount of heating, this would be expected. Since the highest temperature recorded in the estuary at low tide was 36°C (Macnae 1957), these five species appear to be living well within their upper lethal temperatures for rapid heating. The long term experiment indicated that *Dosinia* and *Macoma* could live at temperatures up to 36°C and 34°C respectively. The highest temperature recorded in the open waters of the estuary was 28°C, and because the temperature change beneath the surface of the substrate, where these bivalves occur, is less than that on the surface (Duff & Teal 1965, Johnson 1965), they thus appear to be living well below their lethal temperatures.

The temperature tolerances of estuarine animals vary seasonally, the animals being acclimated to, and thus tolerating, higher temperatures during summer than during winter (Evans 1948, Todd & Dehnel 1960). The animals used in these experiments were studied just after the end of summer and their upper lethal temperatures were therefore probably at their maximum values.

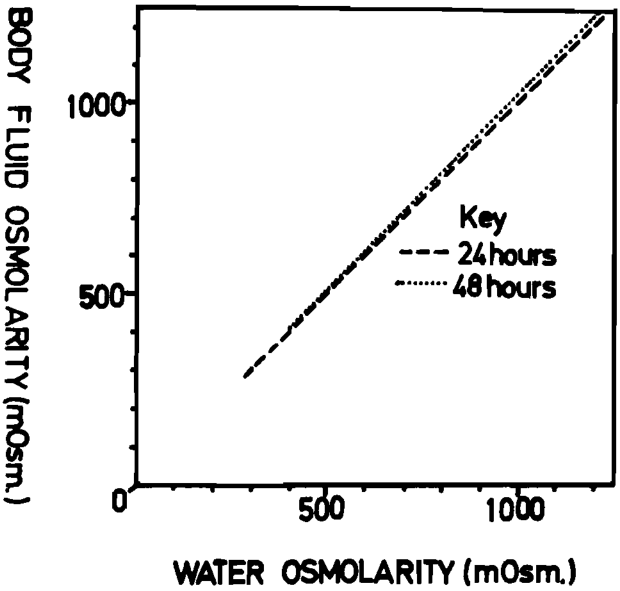

FIGURE 2

Body fluid concentrations vs. concentration of the medium in *Solen capensis* after 24 and 48 hours immersion in a range of salinities. All animals acclimated to sea-water (1 070 mOsm). Regression lines:

24 hours: Y = −1,73 + 1,016X. S.D. = 0,088
48 hours: Y = −8,26 + 1,034X. S.D. = 4,765

Salinity Tolerances and Osmoregulation

All of the species studied appear to be euryhaline osmoconformers, capable of tolerating greater salinity ranges than they normally encounter, except during flood conditions. This tendency has also been found in other bivalves by Beadle (1957), Castagna & Chanley (1966), Pierce (1970) and Wilson (1968). Species whose valves gape appear to tolerate dilution or concentration of their body fluids within their non-lethal salinity ranges. Examples of such species are both the species of *Solen* studied and *Macoma litoralis*. *Dosinia hepatica* tolerates dilution of its body fluids over its non-lethal salinity range, but escapes salinities below (and above) its non-lethal range by tight closure of its valves.

From Figures 1 and 2 it can be seen that over their non-lethal ranges (from about 13‰ to at least 42‰), the body fluids of both species of *Solen* equilibrate to the concentration of the medium within 24 hours. Below this range equilibration is slower and is followed by death. In this respect it was noticeable that *S. corneus* was slightly more tolerant of low salinities than *S. capensis* (cf. Figures 1 and 2). The non-lethal range for *Dosinia hepatica* extends from approximately 14‰ (420 mOsm) to at least 45‰ (1 350 mOsm). Below this range it remains tightly closed, and equilibration occurs extremely slowly, so that after 23 days in distilled water specimens still had water of 22‰ (660 mOsm) in their mantle-cavities and only 25% mortality had occurred. The

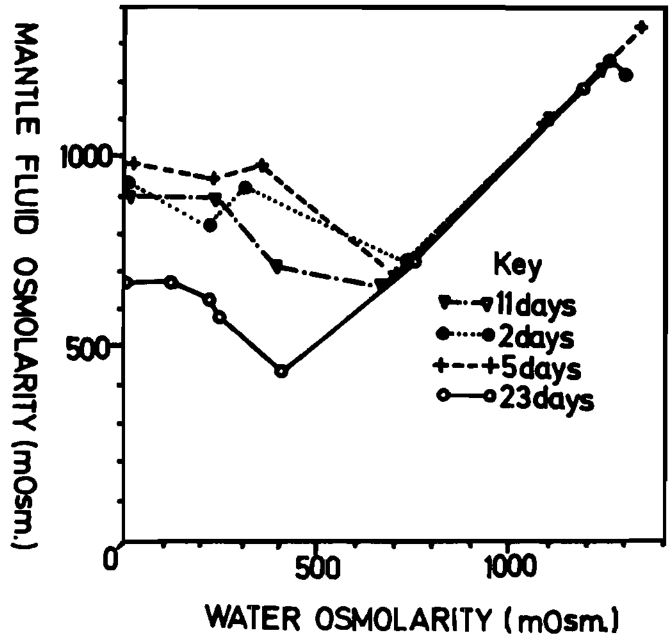

FIGURE 3

Concentrations of the mantle cavity fluids after 2, 5, 11 and 23 days immersion in different salinities in *Dosinia hepatica*. All animals acclimated to sea-water (1 070 mOsm).

pH values of the mantle-cavity fluids after these 23 days were close to 7,0 in all specimens. This was on average about 0,9 pH units lower than the dish-water pH (Table 3). This lowering of pH is probably due to accumulation of CO_2 and acids produced by the animals while closed. In the case of *Macoma litoralis* the non-lethal range extended down to 7‰ (210 mOsm). As *Macoma* has a small posterior gape to its valves it equilibrates faster than *Dosinia* but compensates for this by having a greater non-lethal salinity range. The higher pH values recorded for the mantle-cavity fluids of *Macoma* than *Dosinia* are no doubt due to the presence of this gape, which allows some outside water to enter the cavity and gases to diffuse out.

Under normal conditions in the estuary all of these bivalves would thus be functioning within their salinity tolerance limits. During floods, however, the position is different. Here the ability to escape the lowered salinities is important. Of the three common species in the middle reaches of the estuary, *Dosinia hepatica* appears best adapted to this, followed by *Macoma litoralis* and *Solen corneus* in order of increasing gape and more rapid equilibration. The upstream distribution of these three bivalves into areas of lowered salinities, occurs in the same order, with *Dosinia hepatica* penetrating the furthest and *Solen corneus* the least (McLachlan & Grindley in press). Minor floods, lasting only a day or two, could probably be tolerated by all of the above species, but more severe floods, such as recorded during April 1971 could have a serious effect.

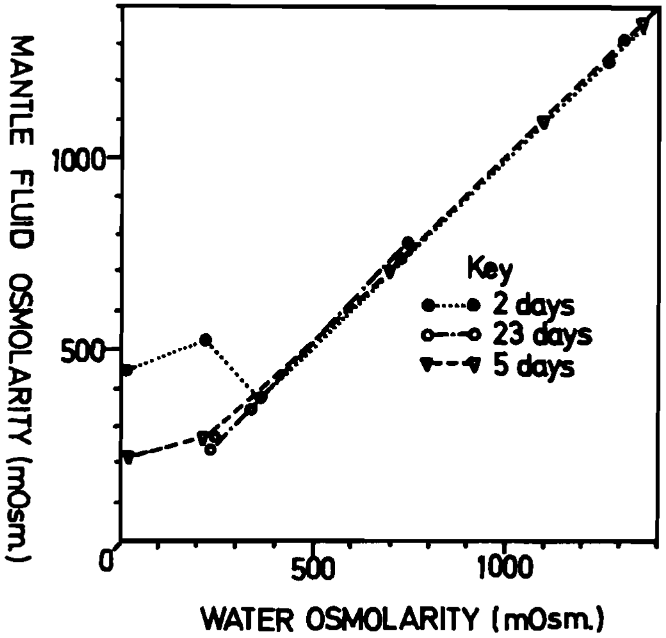

FIGURE 4
Concentrations of the mantle cavity fluids after 2, 5 and 23 days immersion in different salinities in *Macoma litoralis*. All animals acclimated to sea-water (1 070 mOsm).

In fact, dead specimens of both *Macoma litoralis* and *Solen corneus* were found in the middle reaches of the estuary after these floods. As fluctuations in salinity are greatly reduced within the substrate the bivalves would to some extent be insulated from the lowered salinities. They would nevertheless be forced to come into contact with lowered salinities if they attempted feeding. Furthermore, as floods often tend to scour the surface of the substrate they might, during severe floods, be virtually exposed to the overlying water.

No attempt was made to assess the effect of age or different acclimation salinities on the tolerances of these species. It can, however, be stated that no differences were noticed between mortality rates of different-sized specimens. The interaction between temperature and salinity effects has also not been studied.

Both species of *Solen* and probably also *Dosinia* and *Macoma* appear to be osmoconformers in the sense that the concentrations of their body fluids parallel the concentrations of the fluids in their mantle-cavities (Figures 1 and 2), which in turn may or may not be the same as the external medium. In both species of *Solen* the body fluids are always slightly hyperosmotic to the medium, and this hyperosmotic tendency increases slightly from 24 to 48 hours after immersion in different salinities. This supports the findings of Freeman & Rigler (1957) and Pierce (1969, 1970 and 1971) that bivalves are hyperosmotic osmoconformers, though Wilson (1968) found the body fluids of *Xenostrobus* to be slightly hypoosmotic with respect to the medium.

An interesting point arising out of these studies on temperature and salinity tolerance in bivalves is the effect of the shell structure and amount of gape on tolerance limits. The disadvantage of gape is that it exposes the animal to the environment. This has already been mentioned as far as salinity tolerances are concerned. Its relationship to temperature tolerance is worth discussing briefly. Just as an increased gape increases the rate of equilibration with the salinity of the medium, so it also increases the rate of thermal equilibration. At very slow rates of heating this effect would probably be absent, but at the rate of 1 C°/10 minutes it was quite noticeable. *Dosinia hepatica* has a round strong shell without any gape. Its upper lethal temperature at this rate of heating is 45,5°C. The valves have a noticeable insulating effect and a large specimen when heated to 40°C at a rate of 1 C°/10 minutes initially has an internal temperature 2,2 C° lower than the medium. *Macoma litoralis* which has a flatter thinner shell (on average four times lighter than a shell of the same length in *Dosinia*) with a slight gape, tolerates only up to 44°C and has a lag of·1 C° at 40°C. *Solen corneus* has a shell of the same thickness as *Macoma,* but has a large gape and is itself much larger (cf. sizes in Table 2). Its lethal temperature was 44,5°C and it has a lag of 1,2 C° at 40°C. In comparing *Solen corneus* and *Macoma litoralis* it would thus appear that the size effect slightly overrides the gape effect. This size or volume effect is particularly noticeable in *Dosinia hepatica* where small specimens equilibrated faster than large ones (Table 2). This does not appear to have any relation to their positions on the shore (McLachlan in press). The fact that this effect was not noticeable in other species was probably because they are not as round as *Dosinia,* and being more flattened, would thus have a much smaller increase in volume in relation to increase in length.

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