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ION REGULATION IN FRESHWATER AND BRACKISH WATER BIVALVE MOLLUSKS[1]

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The relationship between external salinity and the blood concentrations of Na, Ca, K, Cl, and HCO_3 has been examined for six species of freshwater and brackish-water bivalve mollusks: *Rangia cuneata* and *Polymesoda caroliniana* (oligohaline); *Lampsilis claibornensis* and *Corbicula manilensis* (freshwater); and *Ostrea palmula* and *Polymesoda maritima* (marine euryhaline). The two euryhaline species are osmotic and ionic conformers in media of from 100 to 1,000 mOsM. The oligohaline species are conformers above ambient osmolalities of 100 mOsM; in more dilute media the blood is hyperionic with respect to Na, Ca, K, and Cl. In ambient osmolalites below 20 mOsM, the blood concentrations of Na and Cl, as well as blood osmolality, decrease sharply. Blood Ca and HCO_3 concentrations show a concomitant increase. The two freshwater animals are conformers above, and regulators below, 100 mOsM. There is no decrease in the blood concentrations of Na or Cl in very dilute media.

INTRODUCTION

The horohalinicum is that segment of an estuary with salinities ranging from 3 to 8‰ (90–250 mOsM). It acts as a barrier to colonization of dilute waters by marine species, and of high salinity habitats by freshwater species, and, in fact, can be characterized by its low species abundance (Remane 1934; Khlebovich 1969). The horohalinicum is of major physiological importance to mollusks: any and all mollusks, whether they are brackish-water forms or highly adapted freshwater animals, inhabiting salinities lower than 3–8‰ show hyperosmotic regulation of their body fluids (Gainey and Greenberg 1977).

In osmoregulating polychaetes, as external salinity approaches the lower limit of an animal's salinity range, blood osmolality, Na, and Cl fall sharply (see Oglesby [1978] for review). Oglesby (1965) introduced the term "critical low salinity" (CLS) to refer to this point and suggested that it represents the external concentration where mechanisms for ionic regulation begin to fail. The CLS, then, provides a measure of the effectiveness of a species' regulatory mechanisms and hence its tolerance of dilute waters. The CLS has not been applied to mollusks, but Murphy and Dietz (1976) observed changes in blood ionic composition characteristic of the CLS response in the freshwater bivalve *Ligumia subrostrata* during exposure to deionized water. Decreases in the blood concentrations of Na and Cl reduced blood osmolality by 23% after 30 days in deionized water. Hemolymph Ca and HCO_3 increased during the same period.

Several bivalve taxa, including the entire subclass Paleoheterodonta; the families Corbiculidae, Sphaeriidae, Dreissenidae, Asaphidae, Myacidae, and Pholadidae (all subclass Heterodonta); and the families Arcidae, Mytilidae, and Donacidae (subclass Pteriomorphia) include species which are either fully adapted to fresh water or tolerant of habitats within the horohalinicum (Hutchinson 1967; Starobogatov 1970). Since these diverse low-salinity forms evolved independently, there is no reason to presume that their physiological mecha-

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TABLE 1

SYSTEMATIC AND PHYSIOLOGICAL RELATIONSHIPS OF SELECTED BIVALVES

Marine Euryhaline	Oligohaline	Freshwater
Polymesoda maritima (Heterodonta: Corbiculidae)	*Polymesoda caroliniana* (Heterodonta: Corbiculidae)	*Corbicula manilensis* (Heterodonta: Corbiculidae)
Ostrea palmula (Pteriomorphia: Ostreidae)	*Rangia cuneata* (Heterodonta: Mactridae)	*Lampsilis claibornensis* (Paleoheterodonta: Unionidae)

nisms for adaptation to dilute waters are identical.

In this study I have investigated possible variations in these mechanisms as reflected by differences in the response of blood ionic composition to acclimation to dilute media. In addition, the CLSs of those species capable of hyperosmotic regulation have been determined and correlated with the ecological distributions of the animals. The relationship between the ambient salinity and blood concentrations of HCO_3, Cl, Na, K, and Ca in six species of bivalve from four families were examined. The animals include *Lampsilis claibornensis* (Unionidae); *Corbicula manilensis*, *Polymesoda maritima* and *Polymesoda caroliniana* (all Corbiculidae); *Rangia cuneata* (Mactridae); and *Ostrea palmula* (Ostreidae).

The three corbiculids (subclass Heterodonta) constitute a series of species that are adapted to a continuum of salinities from brackish to fresh water. Thus, *P. maritima* lives in marsh salt barrens and tolerates dilute brackish water, but it cannot penetrate the horohalinicum. *Polymesoda caroliniana* is an intertidal-subtidal estuarine species which tolerates fresh water for long periods in the laboratory. Finally, *C. manilensis* usually occurs in fresh water and occasionally in dilute brackish water. These species have been supposed to be a model system, illustrating how adaptations to fresh water could have evolved in the mollusks (Gainey and Greenberg 1977), and should show increasing regulation of blood solutes in the order *P. maritima*, *P. caroliniana*, *C. manilensis*.

Lampsilis claibornensis is a freshwater unionid (subclass Paleoheterodonta); *R. cuneata* is a brackish-water clam (subclass Heterodonta), found in the same habitats as *P. caroliniana* and also tolerant, to some extent, of fresh water. The brackish-water oyster *O. palmula* (subclass Pteriomorphia) is reported to inhabit very low salinities (Bozniak et al. 1969; McCosker and Dawson 1975). Grouping these animals according to the scheme of Gainey and Greenberg (1977), there are two species from different families in each of three physiological categories: marine euryhaline (*O. palmula*, *P. maritima*); oligohaline (*P. caroliniana*, *R. cuneata*); and freshwater (*C. manilensis*, *L. claibornensis*). These relationships are summarized in table 1.

MATERIAL AND METHODS

ANIMALS

Corbicula manilensis and *Lampsilis claibornensis* were collected from the Ochlockonee River, Gadsden County, Florida (0.1 ‰); *Polymesoda caroliniana* and *Rangia cuneata* from the upper reaches of Ochlockonee Bay in Wakulla County (2–6‰); and *Polymesoda maritima* from salt marshes in Wakulla County (28‰). *Ostrea palmula* were collected from rocks in the Miraflores Third Locks Lake in the Panama Canal Zone (12‰).

RESPONSE TO EXTERNAL SALINITY

A series of acclimation media were compounded by mixing water from the Sopchoppy River (Wakulla County) (see table 2 for ionic composition) with seawater from

TABLE 2

IONIC COMPOSITION OF SOPCHOPPY RIVER WATER

π (mOsM)	Na (mM)	Ca (mM)	K (mM)	Cl (mM)	HCO_3 (mM)
3.0	1.1	.3	.05	1.5	.5

the Gulf of Mexico in varying proportions. The osmolalities of the resulting solutions were measured with a freezing-point depression osmometer (Precision Systems Osmette). At least 10 animals were exposed to each acclimation medium in aerated 3-liter aquaria. The media were changed weekly; between changes the osmolality was monitored on alternate days and adjusted with deionized water as necessary. Survival of at least 60% of the animals for 4 wk was taken as indicating successful acclimation to the test medium.

ION ANALYSES

Following the 4-wk acclimation period, blood samples were taken by the method of Pierce (1970): The mantle and extrapallial cavities were drained of fluid, the adductor muscles were slashed, and the hemolymph was collected in chilled centrifuge tubes. The samples were centrifuged at 2,000 × *g* for 10 min to sediment cells and debris, and aliquots of the supernatant were removed for ion analyses and measurement of osmolality. After appropriate dilution, the concentrations of Na, Ca, and K were measured by atomic absorbtion spectrophotometry (Perkin-Elmer 290B). For the Ca determinations, all standards and samples were diluted with a solution containing lanthanum trioxide (0.1%) and HCl (5%); distilled water (conductivity 1.59 μmhos/cm) was the diluent for the other cation measurements. Chloride was measured by titration (Aminco Chloride Titrator, model 4-4417). Bicarbonate ion was determined by the method of Dietz and Branton (1975); i.e., evolution of CO_2 from acidified blood was measured in a respirometer (Gilson GRP-14) and compared to HCO_3 standards.

CLS IN FRESHWATER SPECIES

Ten specimens each of *R. cuneata*, *P. caroliniana*, *C. manilensis*, and *L. claibornensis* were placed in separate aquaria in aerated deionized water. The water was changed daily for 2 wk and a running tally kept of mortality. After 14 days, the surviving individuals were sacrificed and blood collected for analysis as above.

RESULTS

The analysis of *Polymesoda maritima* blood is graphed in figure 1. This species tolerates external osmolalities from 1,000 to 80 mOsM, and shows conformity over the entire range. Blood Na is slightly hypoionic, and Ca is hyperionic at intermediate salinities. The HCO_3 concentration in the blood is relatively constant at all salinities.

The results from *Ostrea palmula* are shown in figure 2. The salinity range is similar to that of *P. maritima*, and the blood concentrations of Na, K, Ca, and Cl conform precisely to ambient over the entire range. Blood HCO_3 is slightly reduced at intermediate salinities.

Blood osmolality and ionic composition in *Polymesoda caroliniana* as functions of salinity are shown in figure 3. This species is tolerant of osmolalities from 1,000 to 3 mOsM (i.e., seawater to river water) and is an ionic and osmotic conformer above the horohalinicum. From 60 to 20 mOsM there is a plateau of hyperionic regulation of the blood, but in river water the concentrations of K, Na, and Cl are sharply reduced. Blood Ca quadruples in animals acclimated to very dilute media (<20 mOsM). Blood HCO_3 does not vary with external salinity.

Rangia cuneata was successfully acclimated to osmolalities from 3 to 600 mOsM (fig. 4). The animal is an osmotic conformer above and hyperosmotic regulator below 80 mOsM. The plateau of hyperionic regulation between 80 and 20 mOsM is not as pronounced as that of *P. caroliniana*, and while decreases in blood Na and Cl occur in animals acclimated to river water, they are not as striking as those in *P. caroliniana*. Blood Ca is more variable in this species and is relatively high at all salinities. Hemolymph HCO_3 is constant above the horohalinicum and increases in more dilute media.

Results from *Corbicula manilensis* are shown in figure 5. These animals tolerated osmolalities from 3 to 400 mOsM; attempts to acclimate them to 600 mOsM were unsuccessful. *C. manilensis* is an osmotic and ionic conformer above the horohalinicum; below 100 mOsM the major blood ions are

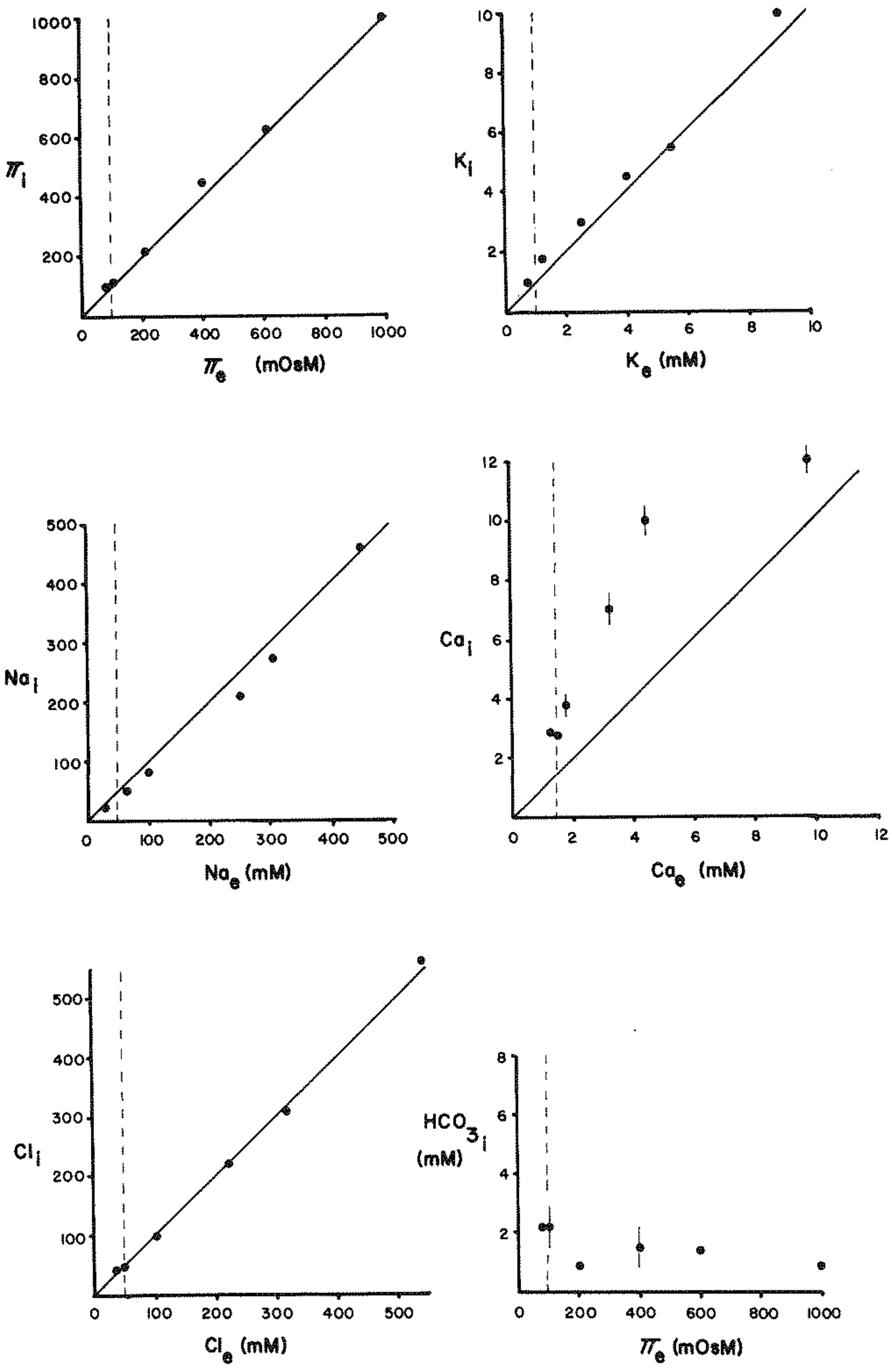

FIG. 1.—Blood ion concentrations in *Polymesoda maritima* as functions of the concentration of the ions in varying media. Each point is the mean of eight blood samples, each sample pooled from two animals. Error bars are ± SD. The dotted line represents the horohalinicum.

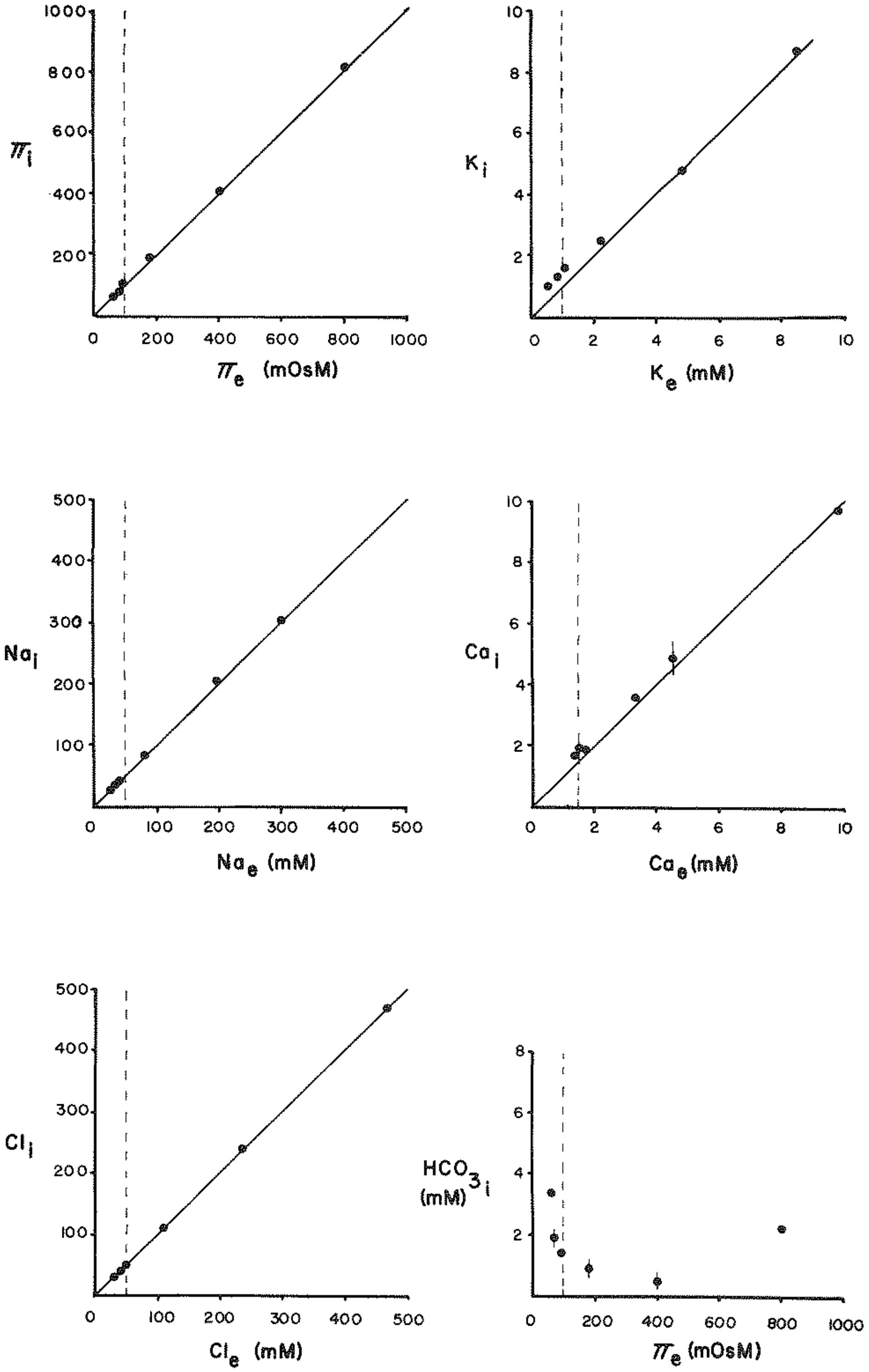

FIG. 2.—Blood ion concentrations in *Ostrea palmula* as functions of the concentration of the ions in varying media. Each point is the mean of eight blood samples. Error bars are ± SD. The dotted line represents the horohalinicum.

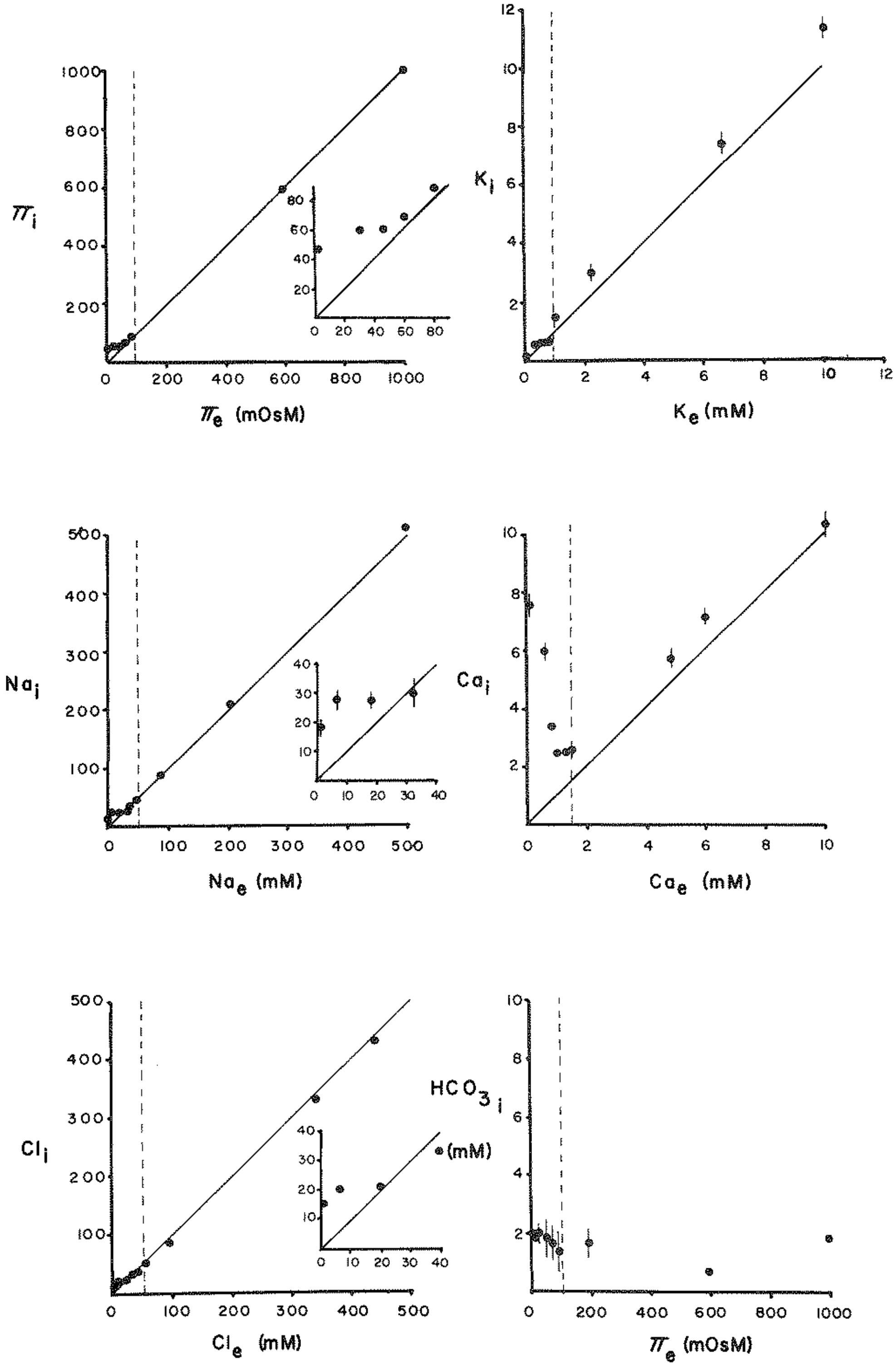

FIG. 3.—Blood ion concentrations in *Polymesoda caroliniana* as functions of the concentration of the ions in varying media. Each point is the mean of eight blood samples. Error bars are ± SD. The dotted line represents the horohalinicum.

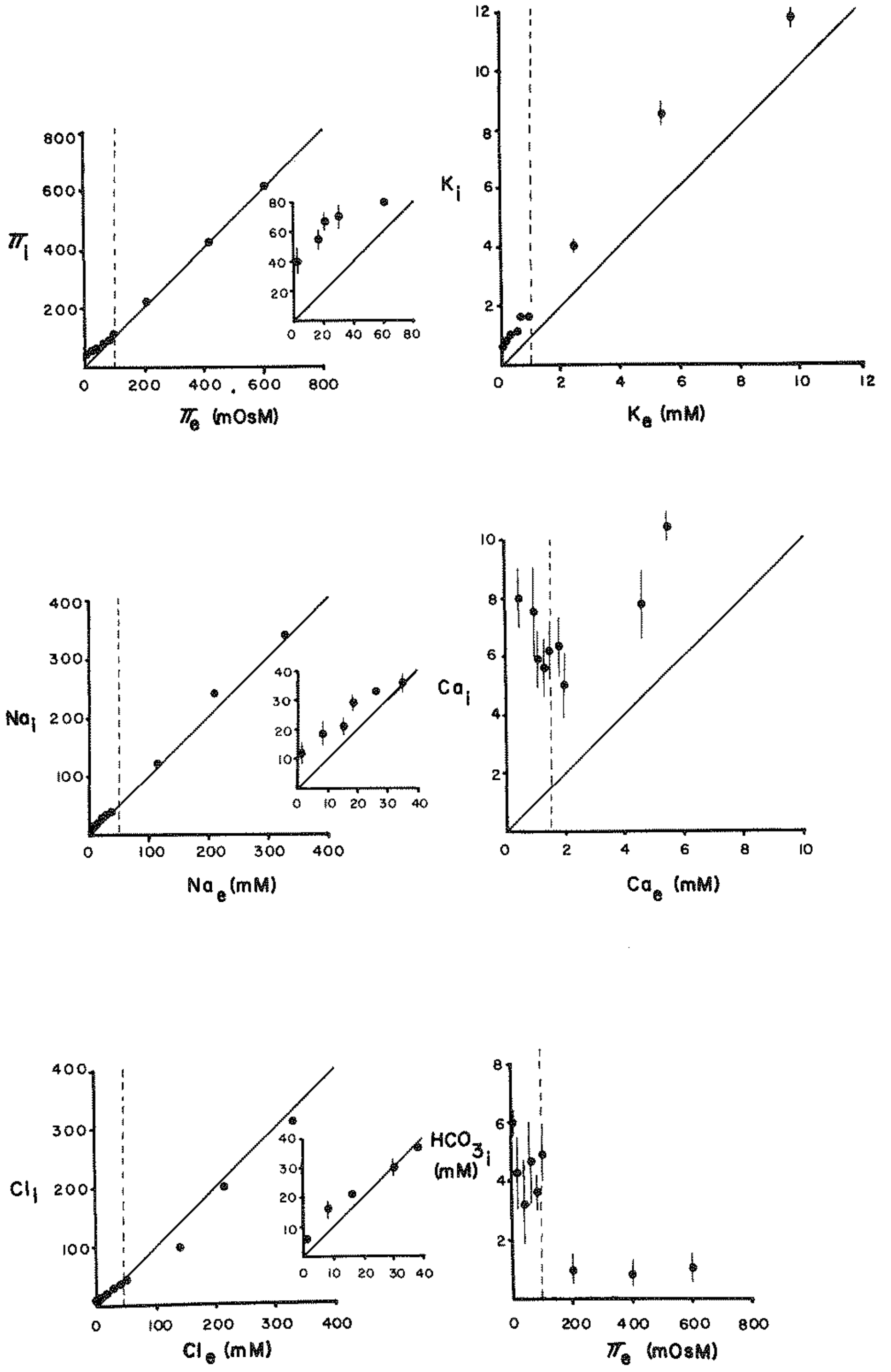

FIG. 4.—Blood ion concentrations in *Rangia cuneata* as functions of the concentrations of the ions in varying media. Each point is the mean of eight blood samples. Error bars are ± 1 SD. The dotted line represents the horohalinicum.

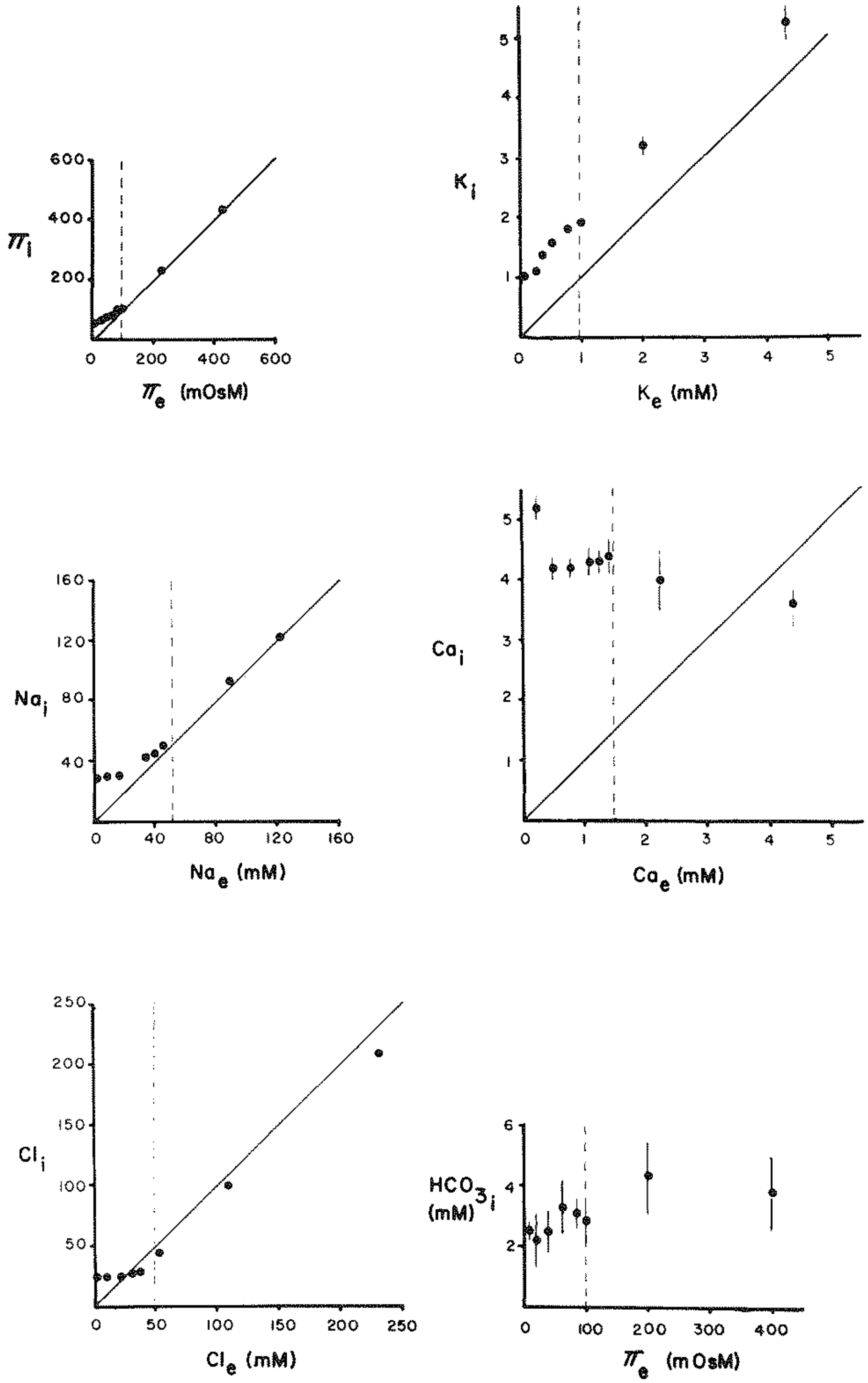

FIG. 5.—Blood ion concentrations in *Corbicula manilensis* as functions of the concentrations of the ions in varying media. Each point is the mean of eight blood samples. Error bars are ± SD. The dotted line represents the horohalinicum.

maintained at concentrations well above ambient. Blood HCO_3 and Ca concentrations do not vary with external salinity.

Lampsilis claibornensis could be acclimated to somolalities from 3 to only 200 mOsM (fig. 6). This species is a hyperosmotic regulator at osmolalities below 60 mOsM. The blood of freshwater-acclimated *L. claibornensis* contains higher concentrations of HCO_3 than the other species studied.

TABLE 3

SURVIVAL OF BIVALVES IN DEIONIZED WATER

Day	*Rangia cuneata* (%)	*Polymesoda caroliniana* (%)	*Corbicula manilensis* (%)	*Lampsilis claibornensis* (%)
1.......	100	100	100	100
2.......	100	100	100	100
3.......	100	100	100	100
4.......	100	100	100	100
5.......	100	100	100	100
6.......	100	100	100	100
7.......	90	100	100	100
8.......	90	100	90	100
9.......	90	100	90	100
10.......	90	100	90	100
11.......	90	90	90	100
12.......	90	80	90	100
13.......	90	70	90	100
14.......	80	40	90	100

The survival of *R. cuneata*, *L. claibornensis*, *P. caroliniana*, and *C. manilensis* exposed to deionized water are shown in table 3. Only *P. caroliniana* was unable to survive in deionized water during the 2-wk test period. This is reflected in the large decreases in the blood osmolality and Na and Cl concentrations in the surviving animals (compare tables 4 and 5). Blood Ca doubles in *P. caroliniana* during exposure to deionized water. The ionic composition of the bloods of *R. cuneata* and *C. manilensis* is little changed by exposure to deionized water, but decreases in blood Na and osmolality did occur in *L. claibornensis* in this medium.

DISCUSSION

Comparison of the response of blood composition to salinities near or below the horohalinicum among the three corbiculid species shows the expected trend of increasing regulation of the blood ions from *Polymesoda maritima* through *P. caroliniana* to *Corbicula manilensis*. Blood ion concentra-

TABLE 4

BLOOD ION CONCENTRATIONS IN BIVALVES AFTER 2-WK EXPOSURE TO DEIONIZED WATER

Species (No.)	Na (mM)	K (mM)	Ca (mM)	HCO_3 (mM)	Cl (mM)	π (mOsM)
Rangia cuneata (8).............	13.5±3.9	.5±.1	10.0±1.5	4.3±.7	6.1±3.9	39.4±6.1
Polymesoda caroliniana (4)......	8.2±4.3	.5±.1	10.9±2.7	2.1±.3	6.3±1.9	21.3±.4
Corbicula manilensis (9)........	23.5±4.7	.8±.1	7.7±2.2	1.9±.5	21.9±1.9	53.3±3.6
Lampsilis claibornensis (10).....	16.4±3.1	.6±.1	4.4±.6	6.6±1.3	11.9±1.3	38.5±2.4

NOTE.—Values are means ± SD.

TABLE 5

BLOOD ION CONCENTRATIONS IN BIVALVES ACCLIMATED TO FRESH WATER

Species	Na (mM)	K (mM)	Ca (mM)	HCO_3 (mM)	Cl (mM)	π (mOsM)
Rangia cuneata..................	11.9±4.4	.5±.1	8.0±1.0	6.0±.4	5.8±1.4	40.8±9.5
Polymesoda caroliniana...........	17.9±5.5	.3±.1	7.6±.8	2.2±.8	14.9±2.4	47.6±2.4
Corbicula manilensis..............	26.7±1.9	1.0±.1	5.2±.5	2.5±.6	24.3±1.4	52.6±7.2
Lampsilis claibornensis...........	27.1±5.0	.9±.1	3.2±.9	6.4±1.3	11.7±2.3	45.9±3.4

NOTE.—No. = 8 for all species, and values are means ± SD.

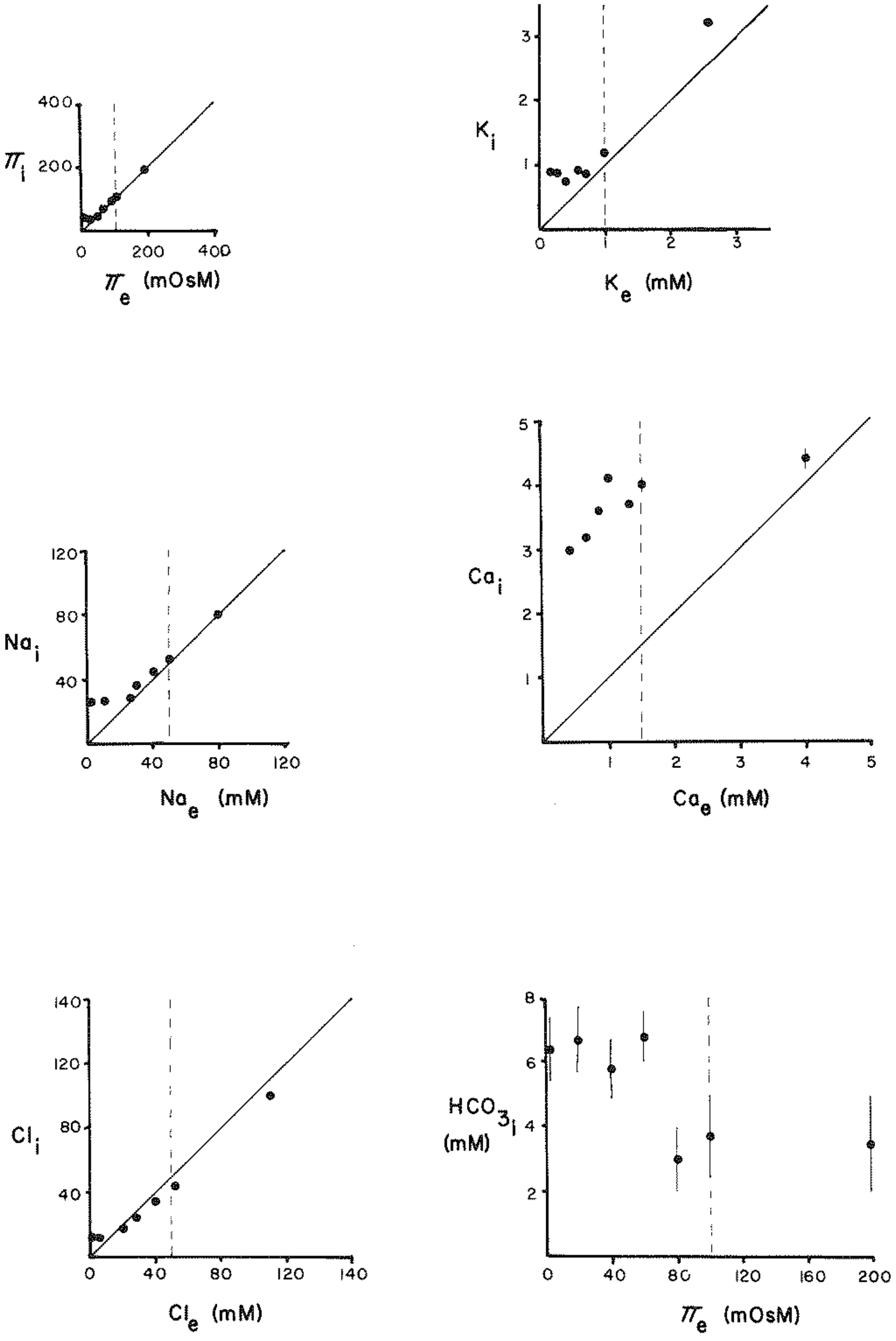

FIG. 6.—Blood ion concentrations in *Lampsilis claibornensis* as functions of the concentrations of the ions in varying media. Each point is the mean of eight blood samples. Error bars are ± SD. The dotted line represents the horohalinicum.

tions in *P. maritima* generally conform to ambient, although there is evidence of hyperionic regulation of Ca at intermediate salinities (fig. 1). Blood Na is hypoionic over the same salinity range. Both *P. caroliniana* and *C. manilensis* regulate blood osmolality, Na, Ca, K, and Cl above ambient in salinities below the horohalinicum (figs. 3, 5). Blood HCO_3 is regulated near the seawater HCO_3 concentration (2 mM) in all of the corbiculid species, and there is no increase in HCO_3 in the blood in dilute media. In *P. caroliniana* exposed to very dilute media (<20 mOsM), blood osmolality, Na, and Cl decrease sharply, while blood Ca rises precipitously (fig. 3). This point (20 mOsM, 0.7 ‰) represents the CLS for *P. caroliniana*. In contrast, *C. manilensis* blood composition is little changed as external osmolality falls below 20 mOsM.

Lampsilis claibornensis also maintains the plateau of hyperregulation of blood osmolality and ions in river water (fig. 6). Blood HCO_3, as in other unionids, is a major anion in the blood (Dietz 1977), and its concentration decreases in animals acclimated to media in which the animals are osmotic conformers. Exposure to deionized water results in perturbations of the blood ionic composition similar to those reported by Murphy and Dietz (1976).

The response of *Rangia cuneata* to dilution resembles that of *P. caroliniana*. While the regulatory plateau is not as well defined as that of *P. caroliniana*, the CLS for *R. cuneata* is also 20 mOsM, since the blood of animals acclimated to river water displays the characteristic decreases in osmolality, Na, and Cl, with a concomitant increase in Ca. *Rangia cuneata* in dilute media maintain higher concentrations of HCO_3 in the blood and are more resistant to short-term exposure to deionized water than are *P. caroliniana*. Thus the two species are similar, but not identical, in their responses to dilution.

All of the animals studied, except *Ostrea palmula*, are capable of some hyperionic regulation of blood Ca concentrations when exposed to salinities near or below the horohalinicum. Mangum, Henry, and Simpson (1979) found increased blood Ca in *R. cuneata* exposed to low ambient oxygen. Bivalves undergoing osmotic stress may close the valves and rely on anaerobic metabolism. Such a response would acidify the body fluids and leach $CaCO_3$ from the shell (Dugal 1939). Akberali, Marriott, and Trueman (1977) have observed this behavior in the euryhaline clam *Scrobicularia plana* following exposure to osmotic shock. The shell serves as a sink of Ca and HCO_3 which can be used to moderate hemolymph dilution in osmotically stressed bivalves. At the CLS, however, the decreases in hemolymph Na and Cl are not made up by increases in Ca and HCO_3, resulting in a net decrease in blood osmolality. Hence, Oglesby's criteria for the CLS can be applied to mollusks which osmoregulate. The CLS response appears in freshwater bivalves and gastropods (Little 1965) exposed to deionized water.

The strict ionic conformity of *O. palmula* over its entire salinity range, especially below the horohalinicum, is considerably different from the responses of the other species to dilution. There are far fewer pteriomorph bivalves in dilute habitats than heterodont or paleoheterodont species (Deaton 1979), and the lack of regulation of blood Ca may be an important factor limiting the penetration of low salinity waters by pteriomorph species.

Polymesoda caroliniana does not occur in fresh water (Andrews and Cook 1951; Castagna and Chanley 1973), and while *R. cuneata* has been reported to occur in fresh water, the reports do not include data on the salinity at the purported freshwater habitat (see for e.g., Parker 1960; Pfitzenmeyer and Drobeck 1964). When populations of *R. cuneata* occur in very dilute water, the ambient osmolality is probably above 20 mOsM except during scattered, very brief periods (Hopkins 1969). Clearly, *R. cuneata* is not a freshwater bivalve and is physiologically much closer to *P. caroliniana* than to *C. manilensis* or unionid mussels.

Oligohaline species, such as *P. caroliniana* and *R. cuneata*, can tolerate very low salinities as well as the environmental fluctuations encountered in estuarine habitats. Gainey and Greenberg (1977) suggested that, since oligohaline forms can penetrate the horohalinicum, they are prevented from colonizing fresh water only by their lack of specialized reproductive mechanisms. This idea is probably only partially correct. The difference between river water (3 mOsM) and very dilute brackish water (20 mOsM) seems slight but may be critical to the survival of oligohaline bivalves. Measurements of ion fluxes in unionid mussels and *C. manilensis* show that these freshwater species take up Na and Cl from media with osmolalities as low as river water, and that the uptake of the two ions is independent (Chaisemartin, Martin, and Bernard 1968; Dietz 1979). Comparable measurements have not been made for an oligohaline bivalve, but the striking decreases in blood osmolality, Na, and Cl which occur in *P. caroliniana* and *R. cuneata* at ambient osmolalities below 20 mOsM indicate that these animals are unable to maintain blood ionic composition within acceptable limits in river water. This CLS of 20 mOsM, if general to all oligohaline animals, may serve as a diagnostic criterion to distinguish such species from "true" freshwater forms.

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