Reference: *Biol. Bull.*, 136: 114–129. (February, 1969)

OSMOREGULATORY CAPACITIES OF *CALLIANASSA* AND *UPOGEBIA* (CRUSTACEA: THALASSINIDEA)[1]

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The thalassinid burrowing mudshrimps are an example of a group of decapod Crustacea about which relatively little is known with respect to osmoregulatory capacities. A few pertinent physiological studies have yet to become common coin of the scientific literature. Thus, like several invertebrates of the Black Sea, *Upogebia* (=*Gebia*) *littoralis* was shown to regulate its osmotic concentration in brackish waters (Zenkewitch, 1938). Recent unpublished research demonstrated the strong osmoregulatory capacities of the African mudshrimps *Upogebia africana* and *U. capensis* (Hill, 1967). On the other hand, it has been reported that *U. affinis* of eastern North America survived dilutions of seawater (SW) only to a very limited extent (Pearse 1945). Limited tolerance to diluted SW was also indicated for *Upogebia* sp. and *Callianassa affinis* of western North America (Gross, 1957). Although no data were given for thalassinids in his study, Gross concluded that both species are osmo-conformers. Subsequently the genera *Callianassa* and *Upogebia* have been characterized as "polystenohaline" Crustacea with ionic and volume regulation but with little or no osmoregulation (Brown and Stein, 1960; Lockwood, 1962; Kinne, 1963).

As burrowers in marine sediments since at least the Cretaceous Period (Milne Edwards, 1861; Borradaile, 1903), callianassid and upogebiid crustaceans are widely distributed and such distributions include estuarine or other brackish situations (Schmidt, 1921; de Man, 1927, 1928; Pohl, 1946; Day, 1967). The distribution of *Callianassa filholi* of Australia and New Zealand suggests that this species may well experience brackish conditions (Devine, 1966). *C. turnerana* of Africa migrates annually or semi-annually from brackish water bays up freshwater (FW) rivers and streams, a phenomenon so marked that the Cameroons derives its name from it (Monod, 1927). *C. kraussi* of Africa has a known salinity range of 1.25–59.5‰ (Day, 1951). Both *C. californiensis* and *U. pugettensis* survived the storm inundation of Newport Bay, California (MacGinitie, 1939). Such accounts suggest the euryhalinity of those thalassinids concerned but published physiological evidence for the osmotic capacities of thalassinid Crustacea is generally lacking.

This study compares osmoregulatory capacities in *Callianassa californiensis*, *Upogebia pugettensis* and *U. affinis*. Preliminary results for *C. filholi* of New

[1] Part of this paper is based on a thesis submitted by L. C. Thompson in partial fulfillment of the requirements for the M. A. at the University of California, Berkeley. Research supported by NSF Grant GB 4792 and NIH Grant GM 13241–01 at the Marine Science Center, Newport, Oregon, and by NIH Fellowship 1-F1-GM-34, 529–01 at the Bodega Marine Laboratory, Bodega Bay, California.

Zealand are included. In conjunction with a study of metabolic adaptation (R. K. Thompson and Pritchard, *Biol. Bull.*, in press), this report contributes physiological information on a systematically unique group of Decapoda having both anomurous and macurous affinities (Borradaile, 1903; Gurney, 1938; Waterman and Chace, 1960).

Materials and Methods

Studies on *C. californiensis* and *U. pugettensis* took place at the Marine Science Center of Oregon State University at Newport, Oregon, during summer, 1966. Animals were collected from the exposed flats of the Yaquina Bay estuary at low tides, transported directly to the laboratory and introduced into holding tanks provided with continuously flowing unfiltered SW. We used animals indiscriminately as collected, excepting those damaged, moribund or in postmolt. Postmolt individuals are recognizable by the softer than usual integument, lighter coloration and cleaner appearance.

Individuals were isolated in compartmentalized aquaria and stepwise acclimated by 20% or 25% SW decrements for 1-day periods, followed by a 3-day acclimation period at the final test salinity. Animals were also introduced directly into 125% SW from the holding tanks and held 3 days. The suitability of the 3-day acclimation interval was established by a study of the time required to reach a new steady state with respect to Cl^- (*cf.* Results). Temperatures of media varied from 13–16° C. Salinity of the laboratory SW for the months June-August, 1966, varied between 33 and 35‰; a salinity of 35‰ was taken to represent 100% SW. Concentrated SW was prepared by means of an electric fan and circulating heater. In this fashion several liters of 175% SW could be prepared within 24 hr and boiling was avoided. In all cases dilutions were made with de-ionized glass-distilled water.

Body fluids were obtained as follows. Animals were removed from the medium, rinsed briefly with distilled water and blotted "dry." Blood was taken by penetration of the thin membrane just posterior to the 5th periopods, using a drawn-out Pasteur pipette. Subsampling and analyses usually proceeded at once, as below. Flame photometer analyses were done at the Department of Zoology, Corvallis. In these cases, diluted blood samples were held overnight at 2° C in 2-ml beakers sealed with Parafilm to restrict evaporation. Urine issuing from the nephropore of the antennal base was collected on Parafilm triangles. The most successful stimulus to micturition was to touch the urinary papilla with a warm blunt probe. This procedure eliminated the possibility of puncture, assuring that the fluid sampled was urine. After at least 0.05 ml was collected, samples were taken from the drop for Cl^- and total osmotic concentration using capillary pipettes (Drummond "microcaps") and Hamilton microliter syringes, respectively. Blood, media and standards were handled similarly. Blood was not filtered.

Body fluid Cl^- was determined electrometrically by a Buchler-Cotlove chloridometer. Cations were determined by a Coleman flame photometer, model 21, with filters for Na^+, K^+, and Ca^{++}. Total osmotic concentrations were determined by the Hewlett-Packard vapor pressure osmometer, models 301A and 302. Salinity was measured either by chloridometer or chemically (Schales and Schales, 1941). Salinities were determined on laboratory SW and habitat water samples. The

apparatus used to obtain burrow and interstitial water samples is described elsewhere (R. K. Thompson and Pritchard, in press).

Upogebia affinis was collected near Cape Lookout in the vicinity of Beaufort, North Carolina, on 5 September 1967 (water temperature 22° C) and airmailed to the University of California Bodega Marine Laboratory where acclimation at 22° C commenced at once. Twenty-seven of 36 animals survived the mailing. Animals were transferred to small plastic trays containing 500 ml of medium, 4 per tray. Water was changed daily and aeration was not provided. Animals were stepwise acclimated by 15%–25% SW decrements for 24 hr and allowed to remain at the final test salinity 48 hr. Sampling and analytic methods, where applicable, are as above. All *U. affinis* specimens were sampled for blood twice in the course of experiments. Data from the first sampling, reported here, represent individuals which had not molted up to the time of sampling. After sampling, individuals were replaced in their appropriate medium in order to observe longer-term effects of reduced salinity. Within 4 weeks all individuals molted once and 3 twice. Data from a second sampling, not reported here, represent postmolt individuals. The thalassinids of this study may be serially sampled in the manner described without apparent ill effect as long as the blood volumes withdrawn are not excessive. However, all data reported here derive from individuals without prior sampling history.

Callianassa filholi was collected at Little Papanui Beach of the Otago Peninsula, New Zealand, on 19 May 1968 (water temperature 11.5° C) and air freighted to the Bodega Marine Laboratory. Eleven of 12 animals survived the mailing and were immediately isolated and introduced into flowing 100% SW. Except for lowered temperature (11–13° C), acclimation methods, sampling and analytic procedures are as for *U. affinis*.

Results

Ecology

C. californiensis is abundant throughout the tidal mudflats of Yaquina Bay, particularly on the south banks, confined to a muddy sand zone corresponding roughly to the 0 to +1 foot tide level. That they are more abundant on the south shore is apparently because of the predominance of sandy beds there. Where such beds extend as spits to lower tidal levels, *Callianassa* commonly occurs, indicating no necessary restriction to the higher intertidal. Near the junction of the Yaquina River with the bay, the abundance of *Callianassa* falls off strikingly, and it is scarce or absent from the river system. A single *C. californiensis* was recovered in McCaffery Slough but the species was not found at several collecting localities within a further distance of 1.8–1.9 kilometers above McCaffery Slough. Thus in the overall estuarine system, the *Callianassa* populations (including those of the congeneric *C. gigas*) appear restricted to the bay.

The beds of *C. californiensis* in the Yaquina Bay system contain numerous apparent openings to the surface. Inspection of the openings, however, revealed that they are without exception occluded with substrate during the period of tidal exposure. Careful digging and probing confirmed the absence of well-formed burrows. In general *C. californiensis* is not found within the top 45 cm of substrate at these times but is abundant at or near the prevailing sub-surface

low water line. These findings are somewhat anomalous, for as one walks over such a bed, watery upwellings spout from the "openings," suggesting burrows. MacGinitie (1934) has described the burrowing activity of *C. californiensis* and has figured a burrow by means of an observation chamber.

When present, the burrows of *C. californiensis* may be regarded as artifacts of recent burrowing activity. At low tides burrows are not buoyed by SW and, in the absence of wall reinforcement, burrows readily collapse. As recently turned-over substrate, however, occluded burrows offer relatively less resistance to the passage of water. This accounts for the spouting seen when pressure is applied by walking over a bed, and also for the relatively rapid drainage of *C. californiensis* beds at low tide (Stevens, 1928). The present findings indicate that (1) patent openings to the surface generally are absent, and (2) the burrow system is relatively impermanent in the natural environment at Yaquina Bay.

U. pugettensis is abundant throughout the Yaquina estuary wherever suitable substrate is present. Within the bay proper the distribution along the northern shoreline is correlated with the presence of alluvium ranging from muddy silt deposits at the Newport Marina to mud-clay of the sloughs. *Upogebia* is generally absent from the sandier southern shoreline of the bay. Unlike *Callianassa, Upogebia* is widespread within the Yaquina River system up to at least Johnson Slough (*ca.* 7 kilometers beyond Yaquina Bay). Within the bay *Upogebia* is most frequently collected at lower tidal levels at the approximate 0 to −1 foot zone; within the river system *Upogebia* is collected from the shallow muddy gravel near-shore areas, the muddy shoreline and high banks of muddy clay along the

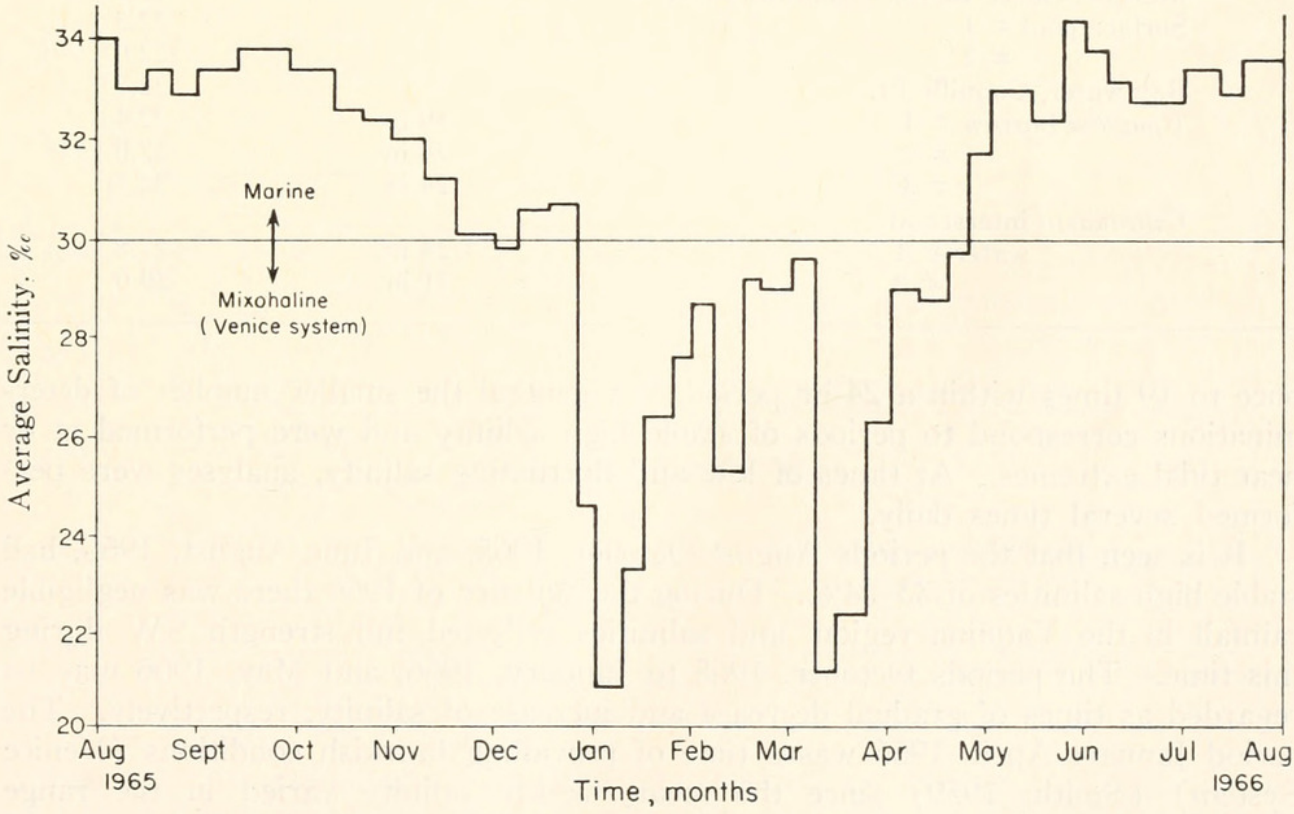

FIGURE 1. Average salinity of Yaquina Bay, Newport, Oregon, for the period August, 1965, to August, 1966. Data through June, 1966, courtesy of the Oregon Fish Commission. See text for explanation.

shoreline, indicating no necessary restriction to the lower tidal zone.

The burrow of *U. pugettensis* has been described (Stevens, 1928; MacGinitie, 1930; R. K. Thompson and Pritchard, in press). We remark only that galleries of the burrow system may penetrate much deeper in the Yaquina region. It is concluded that *U. pugettensis* inhabits a relatively permanent burrow system generally open at the surface.

Salinity of the Yaquina Estuary

Salinity determinations are performed daily at the Marine Science Center. Average salinities for the year 1965–6 are shown in Figure 1. In all cases the data represent bottom salinities of the Yaquina Bay salt water wedge from which the laboratory derives its SW. The intake of the SW system is located approximately where the estuary debouches into the channel leading to the ocean. Salinity values are represented by bars, themselves 7–10 day means of determinations done from

TABLE I

Salinities of water samples taken 11 March 1967 at Yaquina Bay, Newport, Oregon. Surface pool and burrow water samples taken at Coquille Pt. Interstitial water samples taken on the south shore of Yaquina Bay near the laboratory. Values are averages of duplicate determinations

Sample	Depth	Salinity, °/₀₀
Marine Science Center Laboratory SW		28.9
Surface pool # 1		22.5
# 2		22.0
Bay water, Coquille Pt.		22.7
Upogebia burrow # 1	19 in	22.4
# 2	24 in	22.0
# 3	24 in	22.5
Callianassa interstitial water # 1	24 in	27.8
# 2	21 in	29.0

once to 19 times within a 24-hr period. In general the smaller number of determinations correspond to periods of stable high salinity and were performed at or near tidal extremes. At times of low and fluctuating salinity, analyses were performed several times daily.

It is seen that the periods August-October, 1965, and June-August, 1966, had stable high salinities of 33–34‰. During the summer of 1966 there was negligible rainfall in the Yaquina region, and salinities reflected full strength SW during this time. The periods October, 1965 to January, 1966, and May, 1966 may be regarded as times of gradual decrease and increase of salinity, respectively. The period January-April, 1966 was a time of prevailing brackish conditions (Venice System) (Smith, 1959) since the mean weekly salinity varied in the range 21–29.5‰. It may be expected that bottom salinities relatively close to the ocean would not correspond to those of the mudflats further up the estuary during a brackish and labile period. Other studies of the Yaquina estuary show differences

between top and bottom salinities (Burt and McAlister, 1959) and a progressive drop in salinity further up the bay and river system (Frolander, 1964). Quite probably, therefore, animals further up the estuary experience lower salinities than those shown in Figure 1.

Burrow, interstitial and shore water samples (the latter taken at water's edge during ebb tide) were taken periodically from Newport collecting localities during summer, 1966, and salinities determined. Results indicate that without exception resident populations of thalassinids experienced 100% SW during the summer months. On March 11, 1967, following a period of rainfall, samples were again taken at the same Newport localities. Salinity determinations show (Table I) that both species experience brackish conditions. In addition the salinities of samples taken from the burrows of *Upogebia* correspond to those of nearby shore water and surface pools, and that in this particular instance, *Upogebia* experienced relatively more reduced salinity than did *Callianassa.*

Experimental acclimation times

Acclimation times were estimated from experiments measuring the time required to achieve a new steady state with respect to Cl^-. Animals previously acclimated to 100% SW were acutely introduced into 50% SW (Cl^- adjusted to 285 meq/l). Blood Cl^- was monitored for a period in excess of 2 days (Fig. 2). Mean values for the blood Cl^- of the *C. californiensis* and *U. pugettensis* controls kept in 100% SW (Cl^- = 562 meq/l) and sampled at the same time as experimentals are between

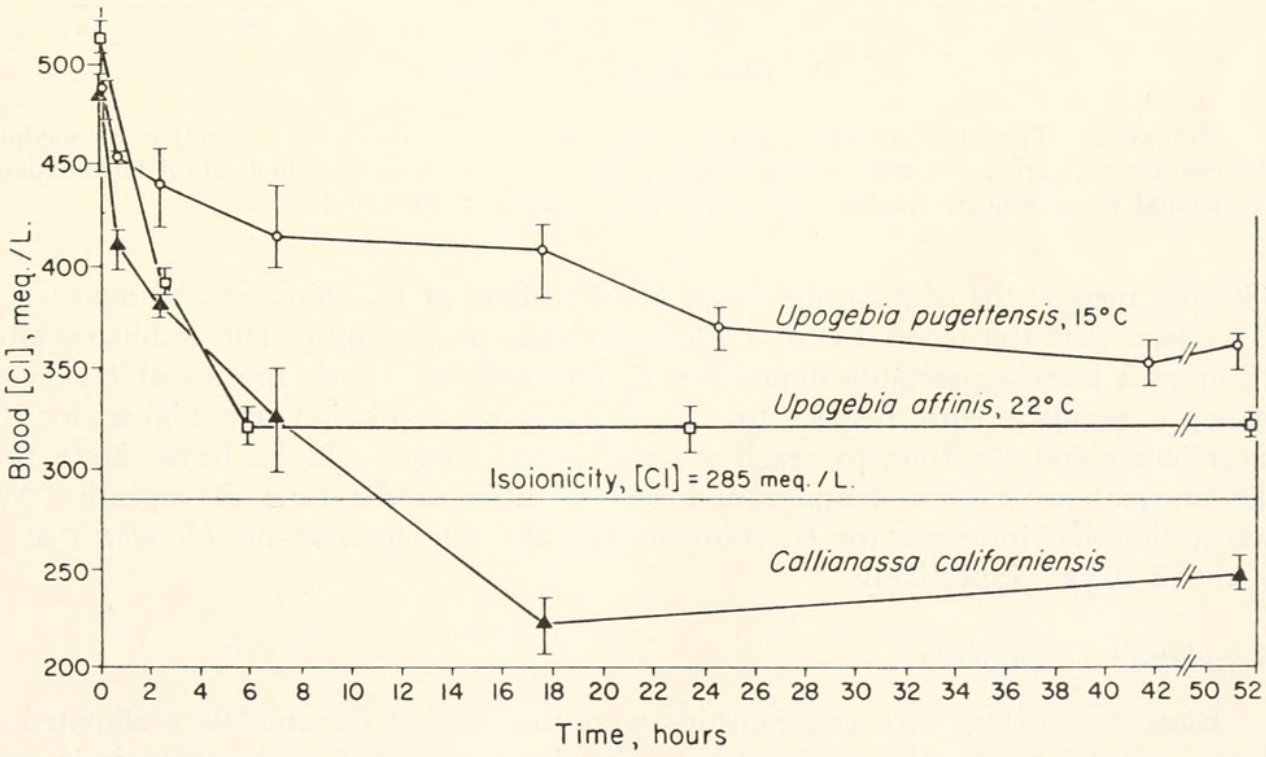

FIGURE 2. Blood chloride concentrations of *Callianassa* and *Upogebia* as a function of time, following acute introduction of animals adapted to 100% SW into 50% SW. ▲ = mean of *Callianassa* Cl, n = 5 at each point; temperatures varied between 13° and 16° C. ○ = mean of *U. pugettensis* Cl, n = 7 at each point. □ = mean of *U. affinis* Cl, n = 3 at each point. Ranges are indicated by vertical bars.

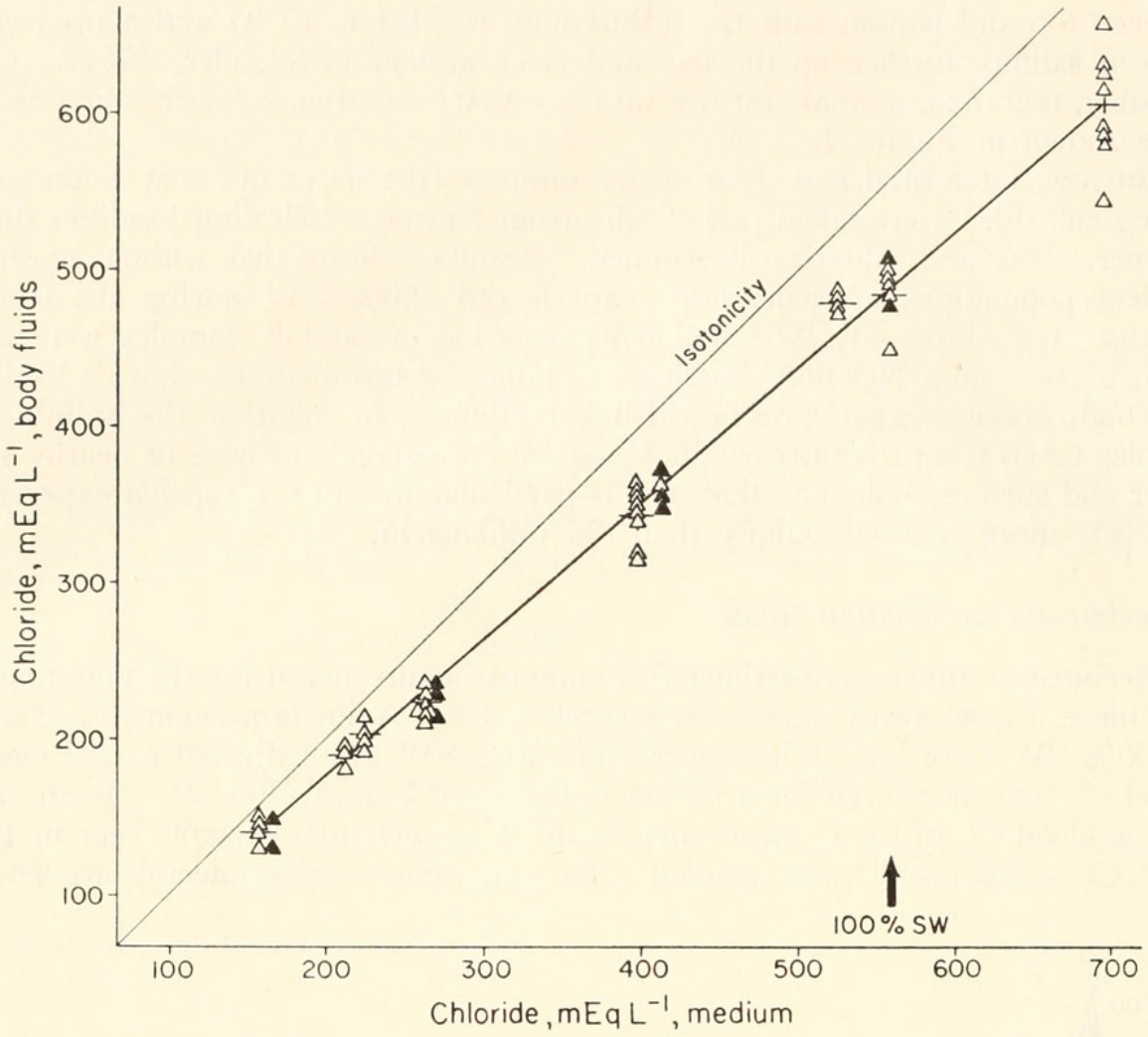

FIGURE 3. The chloride of *C. californiensis* blood and urine as a function of medium chloride concentration. △ = blood; ▲ = urine. Points are averages of duplicate determinations. Horizontal lines indicate means. Temperature of media = 14°–16° C.

480–485 meq/l; the comparable mean for the blood of *U. affinis* is 516 meq Cl^-/l. It is seen that the blood Cl^- of *Callianassa* falls most rapidly but stabilizes after 18 hr at a level appreciably hypo-ionic to the medium. Both species of *Upogebia* strongly regulate with respect to $Cl.^-$ Levels of regulation are higher for *U. pugettensis* and the time to reach a steady state longer (42–52 hr). Note that the unequal acclimation temperatures reflect those of the time of capture. We set acclimation intervals for *C. californiensis, U. pugettensis* and *U. affinis* at 3, 3 and 2 days, respectively.

Regulation of chloride

Blood and urinary Cl^- relationships were determined for animals acclimated to media ranging from 10%–125% SW. The blood Cl^- of *C. californiensis* is consistently hypo-ionic over the range 30%–125% SW (Fig. 3). Urine is iso-ionic to blood with respect to Cl^-. We were unable to collect urine from animals acclimated to 125% SW.

Both species of *Upogebia* regulate Cl^- (Fig. 4). Both are iso-ionic, or nearly

so, in 70% SW ($Cl^- = 395$ meq/l). Between 70%–125% SW Cl^- concentrations for both species are demonstrably hypo-ionic with respect to the medium, and the extent of this hypo-regulation is greater in *U. pugettensis*. Below 70% SW *U. pugettensis* and *U. affinis* strongly regulate the blood concentration of Cl^-, and there appears to be little, if any, difference between the species with respect to the level of regulation. The urine of *U. pugettensis* is iso-ionic to blood with respect to Cl^-.

Mortality and lower lethal limits

The several species proved hardy in the laboratory. In several experiments 3 of 120 *C. californiensis* died in the course of acclimation to media in the range 30%–125% SW, while none of the 11 *C. filholi* died in the stepwise acclimation down to 40% SW. Seven of 147 *U. pugettensis* died in the range 15%–125% SW. Groups of *C. californiensis* and *U. pugettensis* were maintained without loss in 50% SW for more than 3 weeks. Among 27 *U. affinis* there was no mortality in

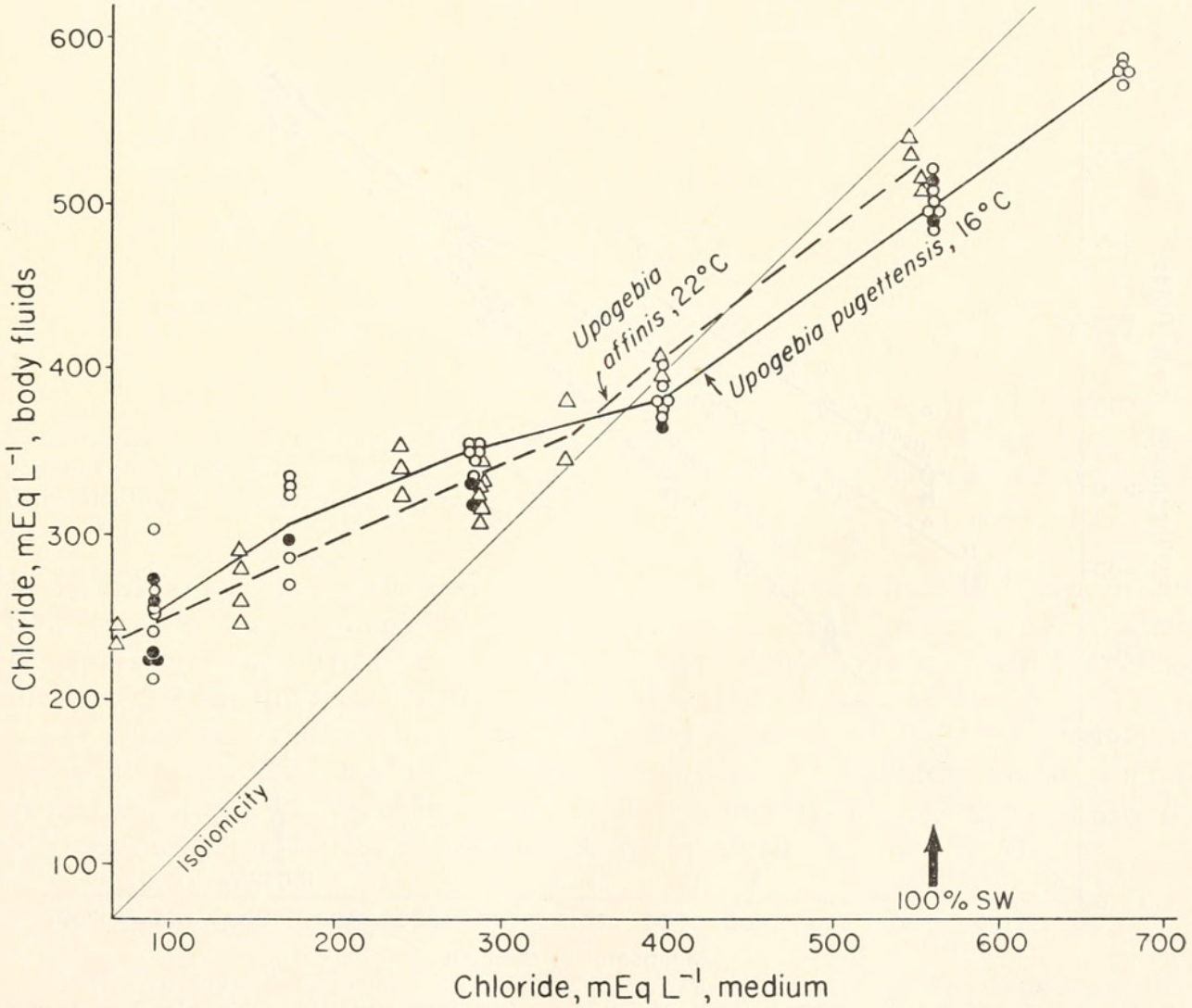

FIGURE 4. The chloride of *Upogebia* blood and urine as a function of medium chloride concentration. *U. pugettensis* blood (○), urine (●); *U. affinis* blood (△). Points are the averages of duplicate determinations.

media ranging from 10% SW to 100% SW. Mortality became pronounced only at salinities less than the lower limits.

Between 25% and 30% SW represents the lower lethal limit for *C. californiensis* under laboratory conditions. Seven animals previously acclimated to 40% SW perished overnight in 25% SW without aeration; 20 animals previously acclimated to 30% SW died overnight in 25% SW with aeration. On the other hand, *C. californiensis* in several experiments survives 30% SW for at least 3 days when provided with aeration, although sluggishness and weakness are manifest. In 125% SW 8 of 9 animals survived 3 days but we did not pursue the upper lethal limit.

U. pugettensis survived 3 days in 15% SW (n = 10) but appeared sluggish;

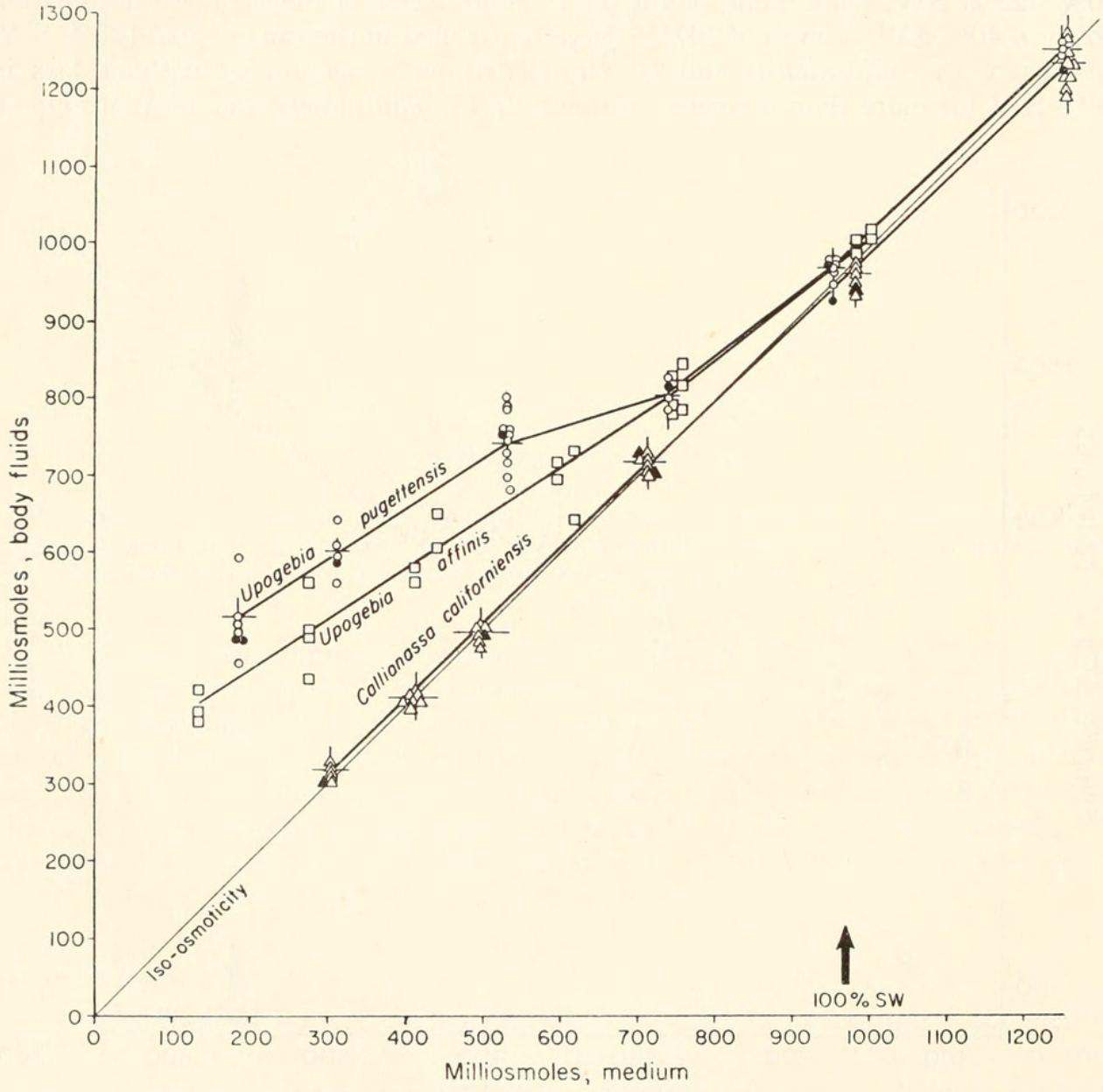

FIGURE 5. Total osmotic concentrations of *Callianassa* and *Upogebia* blood and urine as a function of medium osmotic concentration. *U. pugettensis* (temp. 15° C) blood = ○, urine = ●. *U. affinis* (temp. 22° C) blood = □. *C. californiensis* (temp. 14°–16° C) blood = △, urine = ▲. Means indicated by +.

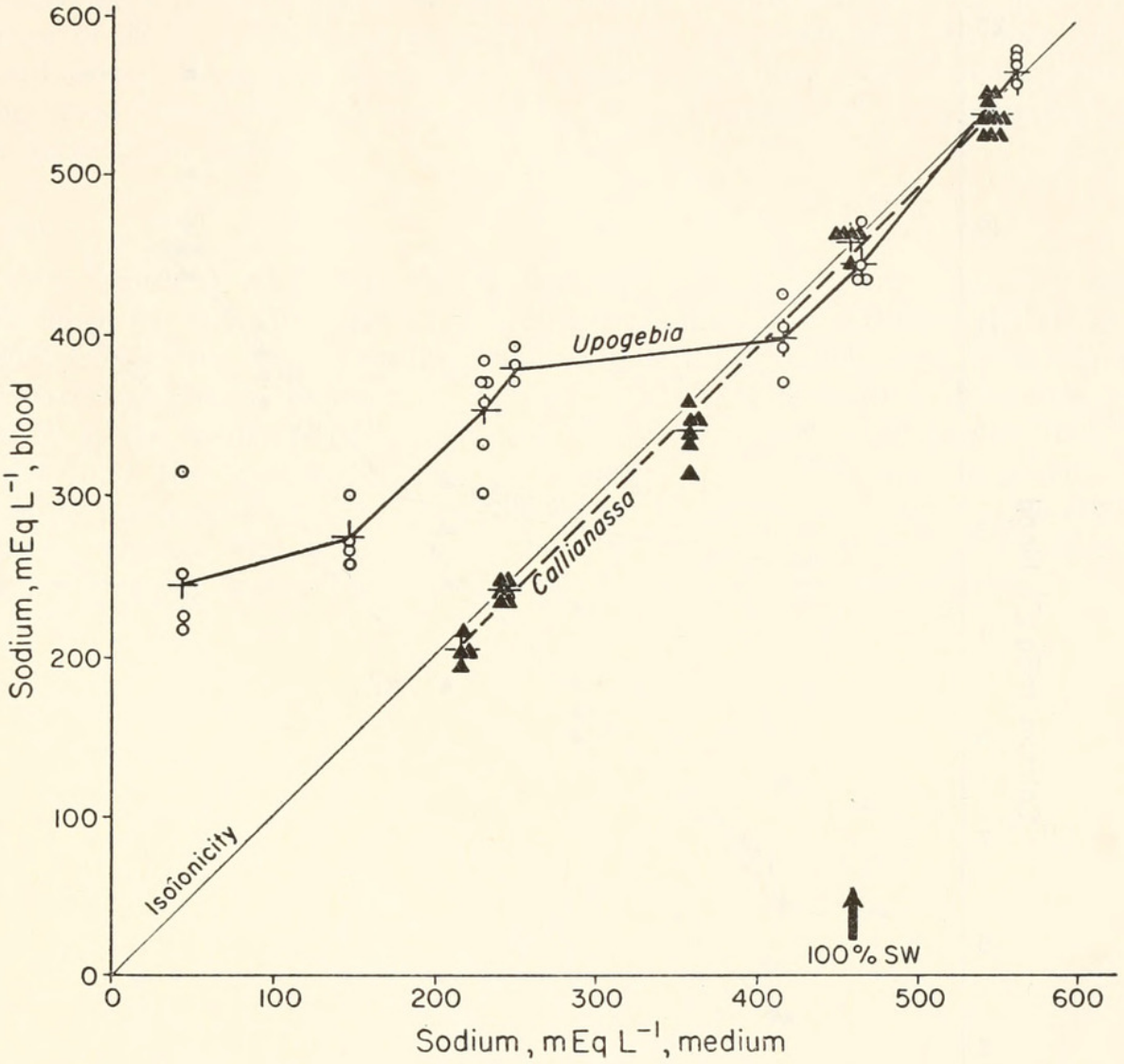

FIGURE 6. Blood sodium of *U. pugettensis* and *C. californiensis* as a function of medium sodium concentration. Temperature of media 15° C. Points represent averages of duplicate determinations. Group means indicated by +.

in 8% SW 7 of 12 animals died within 36 hr. *U. affinis* survived 2 days in 10% SW (n = 4) but 2 animals perished overnight in 5% SW. Three postmolt *U. affinis* survived 10% SW more than 4 days. Under the acclimation regimen, the lower lethal limit for both species of *Upogebia* appears to be *ca.* 10% SW.

C. filholi survived acclimation down to and including 40% SW. Four deaths occurred in 30% SW, 2 in 35% SW and 2 more in 40% SW after holding animals at this latter concentration for 1 week. In preliminary view, between 35%–40% SW appears to be the lower lethal limit for *C. filholi.*

Total osmotic concentration

With respect to blood concentration, *C. californiensis* is an osmo-conformer within its experimental tolerance range (Fig. 5). Where obtainable, urine is iso-osmotic to the blood. Very limited data indicate that the blood of acclimated *C. filholi* is iso-osmotic to the media tested (40%, 60% and 100% SW). Both

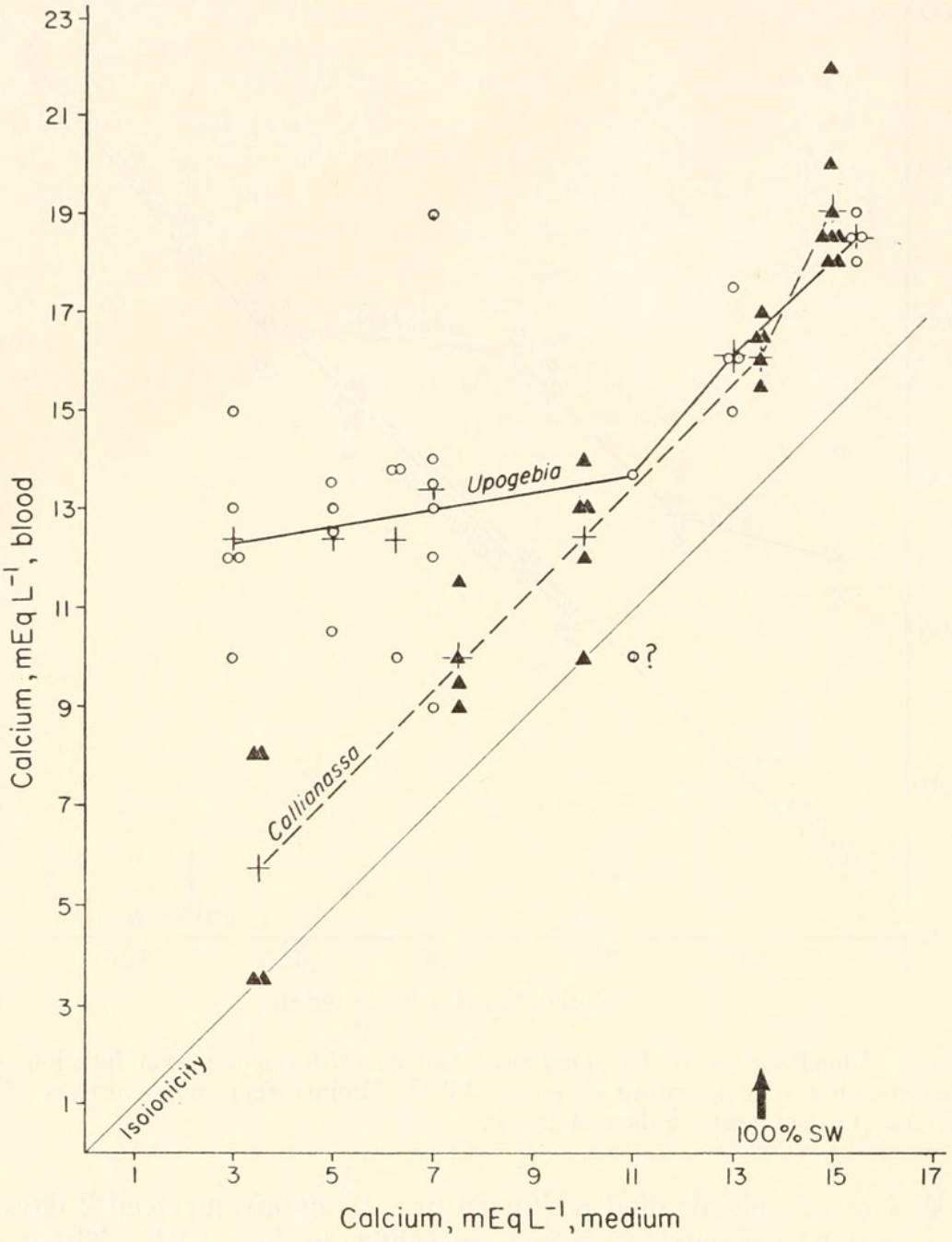

FIGURE 7. Blood calcium of *U. pugettensis* and *C. californiensis* as a function of medium calcium concentration. Temperature of media 15° C. Points represent averages of duplicate determinations. Group means indicated by + with the questioned value omitted.

species of *Upogebia* are iso-osmotic to full strength SW and in *U. pugettensis* this iso-osmoticity extends to 125% SW (Fig. 5). Below 100% SW *U. pugettensis* and *U. affinis* are strong hyper-osmotic regulators. *U. affinis* appears to regulate less well than *U. pugettensis* below 75% SW, although data on the former species are more limited. As in *Callianassa,* the urine of *U. pugettensis* is iso-osmotic to the blood. Data for recently molted *U. pugettensis* are lacking. However, recently molted *U. affinis* survive the range 10%–100% SW for the usual test periods, and measurements indicate that they do so without loss of osmoregulatory ability. As all *U. affinis* molted at least once within a month of their receipt, values

presented here probably represent individuals in various stages of the premolt.

Five of 27 *U. affinis* were parasitized in the right branchial chamber by the bopyrid isopod *Pseudione upogebiae*. Values for Cl^- and total osmotic pressure of the blood were essentially the same as for non-parasitized *U. affinis* with the same acclimation history.

Cations

With respect to Na^+ (Fig. 6), *C. californiensis* is iso-ionic, or nearly so, in media down to 50% SW, but *U. pugettensis* commences regulation of this ion at *ca.* 80%–85% SW. *Upogebia* appears to regulate Ca^{++} comparably (Fig. 7) and *Callianassa* is able to maintain a 2–3 meq Ca^{++}/l concentration difference consistently in the media tested. However, there are large variations in the data on Ca^{++} and the findings should be regarded as preliminary, as should the regulatory patterns of blood K^+ (Fig. 8). Both *C. californiensis* and *U. pugettensis* appear to regulate with respect to K^+, but the stronger regulation of *Upogebia* is irregular, showing marked decreases in K^+ levels in the lower salinities.

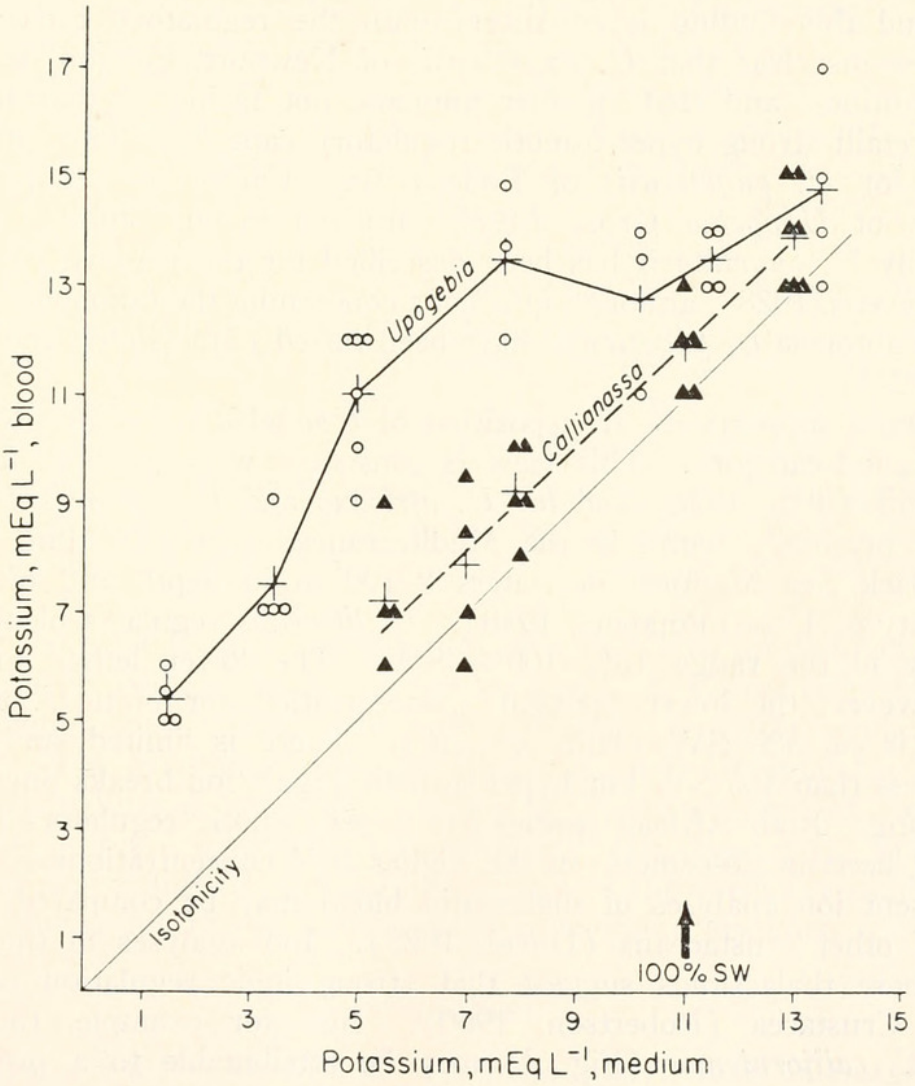

FIGURE 8. Blood potassium of *U. pugettensis* and *C. californiensis* as a function of medium potassium concentration. Temperature of media 15° C. Points are averages of duplicate determinations. Group means indicated by +.

Discussion

Upogebia pugettensis and *U. affinis* resemble certain other characteristically euryhaline Crustacea in their capacity to osmoregulate in dilute brackish conditions. In the higher salinities, both *Upogebia* species conform osmotically, belonging thus to a category of euryhaline crustaceans distinct from those forms which hypo-regulate (Kinne, 1963). Thalassinid urine is iso-osmotic to the blood, a finding not particularly suprising in view of the fact that among decapod hyper-osmotic regulators, distinctly hypotonic urine has been found only in stenohaline FW crayfish (Astacidae), an atyid shrimp (Born, 1968) and palaemonid shrimps (Denne, 1968). Among Peracarida, hypotonic urine has been reported for the amphipods *Gammarus duebeni, G. pulex* and *G. fasciatus* (Lockwood, 1961; Werntz, 1963). The fact that salts are not recovered from thalassinid urine does not imply that the antennary organs of these forms are devoid of osmo-regulatory function. Thus in *U. pugettensis* the antennary organs appear to be necessary for the removal of water whose entry is favored by the maintained osmotic pressure differences and by a relatively high permeability to water (Thompson, unpublished).

Contrary to Pearse's (1945) report, *U. affinis* survives reductions in salinity quite well and this finding is consistent with the regulatory capacities of this species. It seems clear that *U. pugettensis* of Newport, Oregon, is exposed to brackish conditions, and that summer animals, not facing at that time osmotic emergency, retain strong hyper-osmotic regulatory capacity. The same may also be reported for *U. pugettensis* of Bodega Bay, California. It is not known what species of *Upogebia* Gross (1957) utilized in his study. Above Baja California only *U. pugettensis* has been described for the western coast of North America (Stevens, 1928), although questions concerning the taxonomic distinctness of southern California *U. pugettensis* have been raised (MacGinitie and MacGinitie, 1949, pp. 292–3).

The evidence supports the transposition of *Upogebia* from the polystenohaline to the euryhaline category. This view is consistent with the data for *Upogebia littoralis* (Zenkewitch, 1938) and for *U. africana* and *U. capensis* (Hill, 1967). *U. littoralis,* originally found in the Mediterranean Sea (de Man, 1927), is a dominant Black Sea life-form in waters 8–100 m in depth and of an average bottom salinity of 17‰ (Popovici, 1940). *U. littoralis* regulates blood concentration strongly in the range 13%–100% SW. The lower lethal limit was not stated. However, the lower "critical" concentration for both *U. africana* and *U. capensis* is *ca.* 5% SW (Hill, *loc. cit.*). There is limited survival in concentrations less than 5% SW but hyper-osmotic regulation breaks down and death follows molting. Both African species are hyper-osmotic regulators in the lower salinities but become iso-osmotic in the higher SW concentrations.

The present ion analyses of thalassinid blood may be compared to those on the blood of other crustaceans (Duval, 1925). Ion analyses in the iso-osmotic ranges of these thalassinids suggest that strong ionic regulation occurs, as is common in Crustacea (Robertson, 1960). But, for example, the Cl^- hypo-ionicity of *C. californiensis* (Fig. 3) may be attributable to a protein anionic component. Nothing really conclusive on the extent of ionic regulation can be advanced until physico-chemical equilibrium values and transepithelial potentials are measured. Tentatively, therefore, it appears that in *C. californiensis* and

U. pugettensis, Na^+ is at or near equilibrium values, as shown for the eurythaline crab, *Hemigrapsus nudus* (Dehnel and Carefoot, 1965). Over the regulatory range of *U. pugettensis,* the evidence suggests that each ion does not make a relatively constant contribution to the osmotic pressure.

C. californiensis and *C. filholi* cannot osmoregulate yet may be regarded as adapted to survive brackish conditions. Tolerance of dilute media is notable: Animals survive at blood concentrations equivalent to 30% SW or above. Comparatively, the stenohaline marine crabs *Maia squinado* and *Hyas araneus* perish in less than 80% SW and 50% SW, respectively (Duval, 1925; Schlieper, 1929). The anomuran beach crab, *Emerita,* the kelp crab *Pugettia* and some cancroid crabs cannot tolerate less than 75% SW (Gross, 1957). Regarding the whole animal response to osmotic challenge, a second possible factor in survival is delayed time to acclimation. Thus the Cl^- loss rate of *C. californiensis* indicates that, with respect to this ion, a steady state is attained after 18 hr, contrasted to 2 hr for *Emerita* and *C. affinis* (Gross, 1957). A more satisfactory comparison would perforce assess the effects of size and permeability properties upon the rate of equilibration.

An additional factor important for the survival of *Callianassa* is that contacts with the aquatic environment are minimized (*cf.* Kinne, 1967). *C. californiensis* does not possess a well-formed burrow system open at the surface, nor does this species appear dependent upon the integrity of a burrow system for food-gathering (MacGinitie and MacGinitie, 1949) or respiratory functions (R. K. Thompson and Pritchard, in press). The limited data of Table I support the idea that *Callianassa* may be protected from lower interstitial salinities at times of overflowing brackish waters (Reid, 1932) and experience greater salinity stability owing to occupancy of the upper levels of the flats (Milne, 1938).

Since, however, the burrows of *Upogebia* are open to the surface, *Upogebia* is probably more directly exposed to the shallow mudflat waters and consequently to the low and labile salinities of winter and spring. The adaptation of *Upogebia* appears dependent upon the burrow system. Thus the suspension-feeding *Upogebia* (Jørgensen, 1966, p. 88), enclosed in hypoxic or anoxic mud, circulates water through a durable burrow system subserving respiratory and food-gathering functions.

We wish to thank Ralph I. Smith and John W. Born for their critical reading of the manuscript, William Breese of the Oregon Fish Commission for generously providing Yaquina Bay salinity data, and B. J. Hill for kindly sending microfilms of his thesis. The assistance of Cadet Hand, Jr., and Georgiandra Little in the collecting and mailing of the exotic species of this study and of Emily Reid in preparing the figures is gratefully acknowledged. To Rogene K. Thompson goes the credit for suggesting the comparative study of the Newport mudshrimps and to Armand Kuris, our thanks for help on taxonomic questions.

Summary

1. *Callianassa californiensis* and *Upogebia pugettensis* (Crustacea: Thalassinidea) have been studied with respect to their osmoregulatory capacities and selected aspects of their natural history. *Upogebia affinis* and *Callianassa filholi* have been studied with respect to their osmoregulatory capacities.

2. *Upogebia pugettensis* has a discrete, open and durable burrow system and is distributed further up the Yaquina estuary than is *C. californiensis,* which is without such a burrow system.

3. Resident species of thalassinids are exposed to brackish conditions in the winter and spring at Yaquina Bay.

4. The lower lethal salinity limit for *U. pugettensis* and *U. affinis* is approximately 10% SW; that for *C. californiensis* is 25%–30% SW; that for *C. filholi* is probably 35%–40% SW.

5. *U. pugettensis* and *U. affinis* are strong hyper-osmotic regulators below 75% SW. In full strength SW, *U. pugettensis* and *U. affinis* are iso-osmotic, and the former species conforms osmotically in 125% SW. In *U. pugettensis* the ions of Na^+, K^+, and Ca^{++} are comparably regulated, while Cl^- is probably hypo-regulated in the higher salinities.

6. *Callianassa californiensis* conforms osmotically in the range 30%–125% SW. The ions of Cl^-, Na^+, K^+, and Ca^{++} are relatively poorly regulated. Preliminary findings indicate that *C. filholi* conforms osmotically in the range 40%–100% SW.

7. The urine of *C. californiensis* and *U. pugettensis* is iso-osmotic to the blood.

8. The genera *Callianassa* and *Upogebia* are considered to be euryhaline, but the euryhalinity of the former is more limited.

9. The osmoregulatory capacities of *Upogebia* are considered adaptive to osmotic emergencies which arise, in part, from dependence upon an open burrow system; the osmolability and interstitial habits of *Callianassa* are an alternate adaptive response to its estuarine environment.

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