

BEHAVIOR AND RESPIRATION OF THE BURROWING
SHRIMPS *UPOGEBIA MAJOR* (DE HAAN) AND
CALLIANASSA JAPONICA (DE HAAN)

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A B S T R A C T

The behavior and metabolic rates of two burrowing shrimps, *Upogebia major* (de Haan) and *Callianassa japonica* (de Haan), which live on a tidal flat, were studied. The former is a filter-feeder and has a simple Y-shaped burrow. The latter is a deposit-feeder and continually burrows; this results in a complex burrow morphology. The respiration rate of *U. major* under saturated oxygen conditions was about twice that of *C. japonica*. With decrease in oxygen concentration, the respiration rate of *Upogebia* decreased, while that of *Callianassa* remained at about the same level until the oxygen concentration fell to <30% of the saturation value. The O:N ratio (respiration : NH₄ excretion) of *U. major* was significantly higher than that of *C. japonica*, suggesting a difference in food sources. Under anoxic conditions, *C. japonica* survived 3-4 times longer than *U. major*. The physiological characteristics of the two shrimps may be closely correlated with the differences in behavior of the shrimps within their burrows.

Low oxygen stress is a fundamental problem for animals living in burrows in the sea bottom. Among various behavioral and physiological adaptations, ventilation is commonly adopted in many species, especially in crustaceans. Burrowing thalassinid shrimps, such as *Upogebia* and *Callianassa*, which commonly live on intertidal flats, cannot, however, ventilate the burrow during low tide. Adaptations to hypoxic conditions are necessary for these animals. As suggested by Felder (1979), the burrowing shrimps are "highly specialized for a burrowing existence in shallow, hypoxic, marine substrates, and their tolerance of anoxia is clearly an adaptation to habitat."

Three species of thalassinids, *Upogebia major*, *Callianassa japonica*, and *C. petalura*, occur in estuarine and intertidal flats along the coast of the main island of Japan (Sakai, 1969). The first two are very abundant and may play an important role in modifying sedimentary structures and recycling of nutrients through the sediments (Koike and Mukai, 1983; for *U. pusilla*, Dworschak, 1981).

Physiological adaptations of burrowing thalassinid shrimps to hypoxic and anoxic conditions have been studied in the laboratory with North American species (Farley and Case, 1968; Miller *et al.*, 1976; Torres *et al.*, 1977; Felder, 1979; Pritchard and Eddy, 1979). There are, however, few comparative studies concerning physiological and behavioral differences among burrowing thalassinid shrimps (R. Thompson and Pritchard, 1969; Pritchard and Eddy, 1979).

In this study we report a comparison of physiological characteristics in two burrowing shrimps, *Upogebia major* (de Haan) and *Callianassa japonica* (de Haan), and of their behavior observed in a "limorium," a simulated habitat for benthic infauna.

MATERIALS AND METHODS

Observation of Behavior and Burrowing

The animals were collected from a tidal flat in Yamada Bay, in the estuary of the Orikasa River, located on the northern Pacific coast of Japan. The animals inhabit the intertidal zone near the mean sea level at a height of 70-80 cm above the datum line, and were dug out with a mass of sediment surrounding the burrows. Limoria, 2-3 cm wide, 30-50 cm long, and 30-50 cm high, were made with

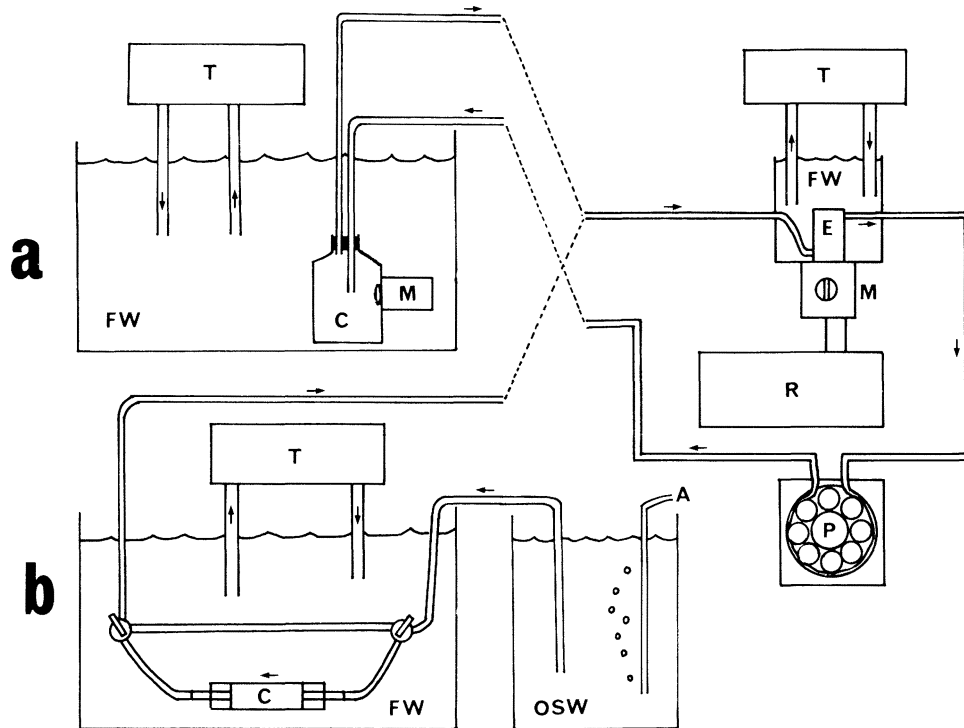


Fig. 1. Apparatus used for measuring oxygen consumption of burrowing shrimps. Arrangement a was used in short duration (20 min) measurements as a closed system; arrangement b was used in long duration (1-2 days) measurements as a flow through system; A, aeration; C, respiration chamber; E, electrode; M, magnetic stirrer; P, peristaltic pump; R, recorder; T, thermoregulator; FW, fresh water; OSW, oxygen-saturated sea water.

transparent acrylic-glass plates (0.5 cm thick). The sediment was transferred into the limoria to make a "sea bottom" 20-30 cm deep, and overlying water (10 cm in depth) was supplied continuously. Burrowing behavior was observed from both sides of the limoria. The structure of the burrow was also examined by taking X-ray photographs of the limoria.

Respiration and Ammonium Excretion

The shrimps used for most of the physiological experiments were collected from Yamada Bay; however, some animals for respiration experiments were obtained from Tokyo Bay. Short-term respiration of the animals was measured with a Clark-type oxygen electrode and the apparatus shown in Fig. 1a. The electrode cell was connected to a respiration chamber (30 ml in volume) by small silicon tubes. The volume of the cell and connecting tubes was 3.5 ml, accounting for approximately 10% of the volume of the respiration chamber. A single animal pre-reared under experimental conditions was transferred to the chamber, and then the chamber was filled with oxygen-saturated filtered sea water (GF/C glass fiber filter) and incubated in the dark. The water temperature was adjusted to that of the natural environment (18.5-22.5°C), where the animals were collected. The salinity of the sea water was approximately 32.6‰. Oxygen decrease was followed for 20-30 min by circulating the sea water with a peristaltic pump at a speed of 4-5 ml min⁻¹, until the oxygen content was reduced to 60-70% of the saturation value. An almost linear decrease of oxygen concentration was observed. The oxygen electrode was frequently calibrated by introducing oxygen-saturated sea water of known temperature and salinity. The oxygen consumption of the filtered sea water was negligible.

The set-up in Fig. 1b was used to measure continuously the oxygen consumption by the animal over 1-2 days. The oxygen-saturated filtered sea water was supplied through the 30-ml incubation chamber (C) at a constant rate (1.5 ml min⁻¹) and the oxygen content in the outflow sea water was continuously monitored with the oxygen electrode. The oxygen concentration in the inflow sea water was also measured periodically.

Ammonium excretion rates were measured using the respiration chamber described above (Fig. 1a). After the respiration experiments, the animal in the chamber was removed immediately. Ammonium concentrations in the sea water before and after the experiment were measured by the indophenol method (Solórzano, 1969). The rate of ammonium excretion was calculated from the volume of the set-up and the increment of ammonium concentration during the experiment. After these experiments, all specimens were stored in a freezer, and later dried at 70°C for 48 h and weighed.

Responses to Hypoxic Sea Water

Respiration rates under the reduced oxygen concentrations were measured by using the same set-up as in Fig. 1a. Oxygen concentrations of 70, 50, 30, and 10% of air-saturation were prepared by bubbling nitrogen gas through filtered sea water for 1–10 min. The animals were preincubated for 0.5 h at the same oxygen concentration, and then used for the respiration measurement. Ammonium excretion by the animals was also measured using the same procedure as described above.

To examine the survival of the animals in anoxic conditions, 10 *Upogebia* and 6 *Callinassa* (one for each bottle) were placed in the glass bottles (130 ml in volume) in the dark. The glass bottle was filled with oxygen depleted sea water (<3% of O₂ saturation) prepared by a procedure similar to that mentioned above. The small amount of oxygen still present should have been consumed within a few minutes by the animal. Every 8 h, the animals in each bottle were examined. The death of each animal was judged from the lack of movement of appendages of the animal when the bottle was turned over. Recovery of individuals which were judged as dead by this criterion was never seen under oxygen-saturated sea water.

RESULTS

Structure of Burrows and Behavior of Shrimps in Burrows

When *Upogebia major* and *Callinassa japonica* were placed on the “sea bottom” in a limorium, they immediately started to dig burrows with their legs. Sediment was dug out, carried with first, second, and third legs, and dumped outside the burrow. The fourth legs were used for cleaning the other legs, oral parts, antennae, and other parts of the body. In *C. japonica*, the entrance of the burrow was narrowed with sediment after initial construction, but such behavior was not seen in *U. major*.

Upogebia major generates a current from the anterior to the posterior of the body by beating its fanlike abdominal appendages, and feeds on suspended particles filtered in a basket made with the setae of the first and second legs and maxillipeds. Similar behavior was reported for *U. pugettensis* (MacGinitie and MacGinitie, 1949). Microscopic observation of the gut contents of *U. major* confirmed the above observation. On the other hand, almost all of the gut contents of *C. japonica* examined consisted of black mud, indicating that it feeds on fine particulate deposit.

The burrow of *U. major* consists of upper and lower parts. The former is fundamentally U-shaped, with two openings to the sediment surface. From the bottom of the U-shaped burrow, a tunnel branches obliquely downwards. In parts of the burrow there are occasional swellings in which the animal turns over. The entrance of the burrow has a slightly narrower diameter than that of the inner part of the tunnel. *U. major* does not make a noticeable mound around the entrance of its burrow.

The burrow of *C. japonica* has a complicated morphology with a rather indefinite shape, as reported for the burrow of *C. californiensis* by MacGinitie (1934) and Swinbanks and Murray (1981). The tunnel forks off in two branches at several globular turning points. There are two or more openings to the sea floor, with a craterlike mound around the opening. The neck of the burrow is very narrow and 3–5 cm long in most cases in the limoria.

In field observations in Yamada Bay, the burrows of *U. major* occurred in muddy sand or sandy sediment; on the other hand, the burrow of *C. japonica*

Table 1. O:N ratios ($\bar{x} \pm SD$; by atoms) of *Upogebia major* and *Callianassa japonica* under variable oxygen tensions. Numerals in parentheses indicate the number of specimens examined.

Species	Dissolved oxygen (%) of saturation				
	100%	70%	50%	30%	10%
<i>U. major</i>	20.2 \pm 8.8 (9)	17.4 \pm 8.5 (3)	16.1 \pm 11.9 (3)	16.1 \pm 8.5 (3)	14.5 \pm 6.0 (3)
<i>C. japonica</i>	48.9 \pm 38.5 (5)	67.5 \pm 14.5 (3)	51.9 \pm 32.5 (3)	102.8 \pm 58.7 (3)	32.7 \pm 15.5 (3)

was found on a muddy flat. The burrow wall of *U. major* was coated with a brownish lining, 1–2 mm thick, which was very compact and distinct from the surrounding sediment. The rigid structure of the *Upogebia* burrow suggests that the animal lives without changing the structure of the burrow once formed, as Swinbanks and Murray (1981) suggested for *U. pugettensis*. The burrow of *C. japonica* also had a brownish lining that consisted of finer particles compared to the surrounding sediments. The burrow wall of *C. japonica* was, however, more fragile than that of *U. major*.

Rates of Respiration and Ammonium Excretion

The respiration rate of *Upogebia major* ranged from 0.51 to 1.71 ml O₂ g dry wt⁻¹ h⁻¹ and that of *Callianassa japonica* from 0.19 to 1.11 ml O₂ g dry wt⁻¹ h⁻¹. The weight of shrimps ranged from 0.178 to 0.465 g dry wt for *Upogebia major* and from 0.198 to 0.716 g dry wt for *Callianassa japonica*, respectively. The rate might be negatively correlated with size in both species (but insignificant statistically; Fig. 2). The respiration rate of *U. major* on a dry wt basis was roughly twice as high as that of *C. japonica*.

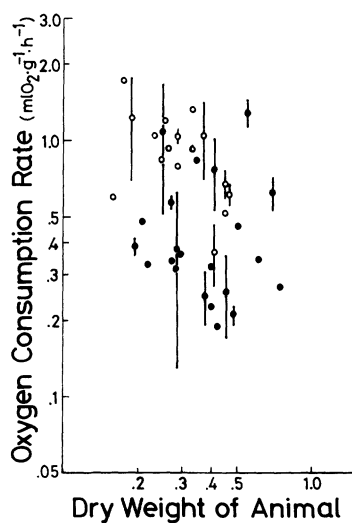


Fig. 2. Rate of oxygen consumption per unit weight plotted against body weight in *Upogebia major* (O) and *Callianassa japonica* (●) on a log scale: if replicate measurements in the same individual were made, results are means; bars represent SD.

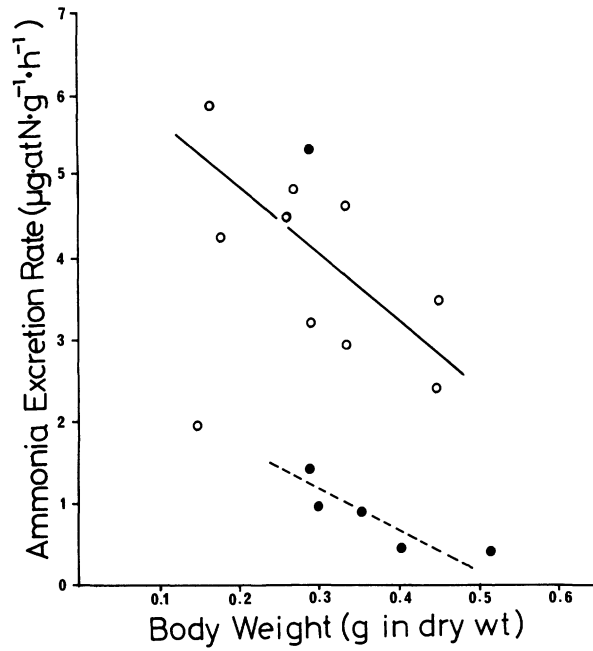


Fig. 3. The relationships between ammonium excretion rate and body weight (dry wt) in *Upogebia major* (○) and *Callinassa japonica* (●).

Diurnal changes of respiration rate were monitored continuously for 35–40 h for both species (*U. major*, $N = 9$; and *C. japonica*, $N = 10$). Correlogram analysis of the results did not detect any significant cyclic phenomenon in either species except for one *Callinassa* which showed a clear 6-h cycle. In both *Upogebia* and

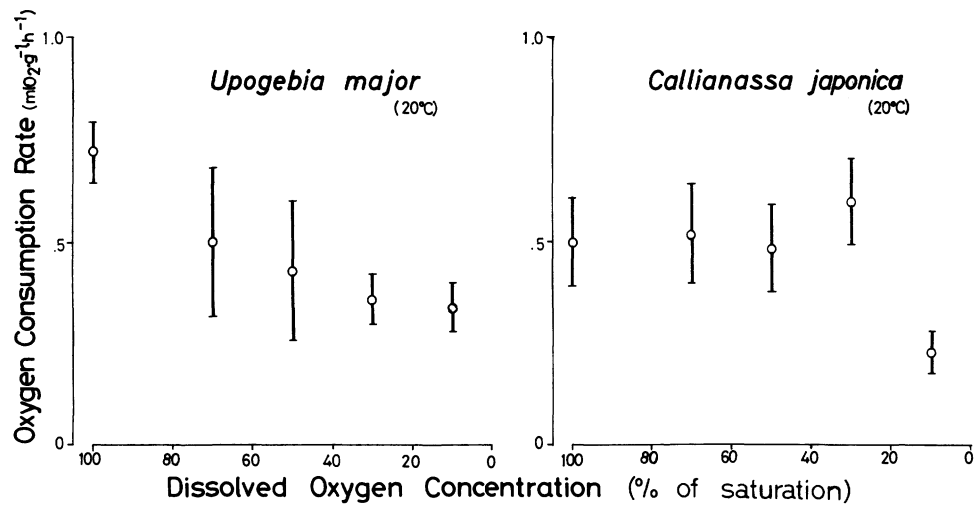


Fig. 4. Changes in oxygen consumption of *Upogebia major* and *Callinassa japonica* with decreasing levels of oxygen saturation in the sea water.

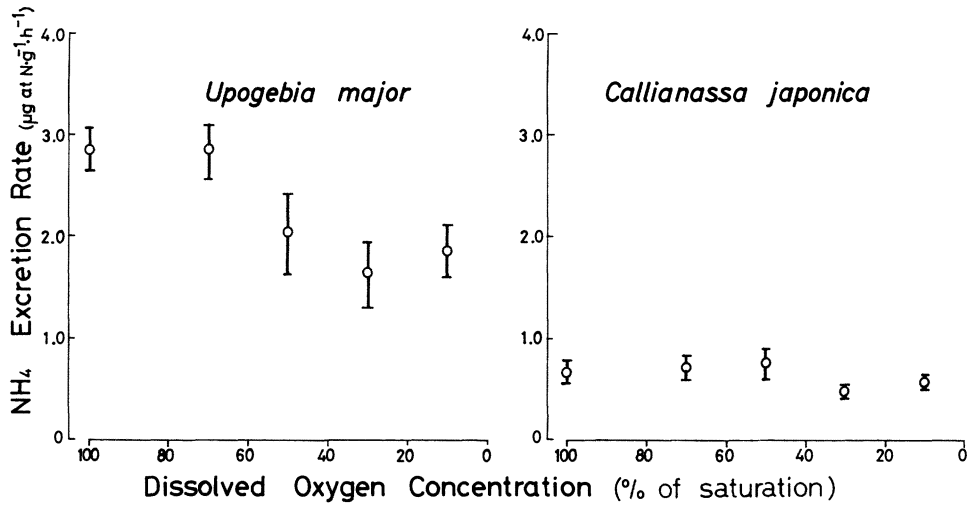


Fig. 5. Effects of lowered oxygen concentration on NH_4 excretion in *Upogebia major* and *Callianassa japonica*; the x-axis shows the oxygen concentrations at the beginning of the experiment. Vertical bars represent one SD of means.

Callianassa, respiration rates fluctuated during the experiments by a maximum of twofold even under dark constant conditions (data not shown).

The rate of ammonium excretion was $2.0\text{--}5.9 \mu\text{g-atomsN g dry wt}^{-1} \text{ h}^{-1}$ in *U. major* and $0.4\text{--}1.4 \mu\text{g-atomsN g dry wt}^{-1} \text{ h}^{-1}$ in *C. japonica* (Fig. 3), if one extremely high value (5.3) for *C. japonica* is excluded. The ammonium excretion rate of *U. major* was about threefold higher than that of *C. japonica* (significant in Mann-Whitney's U-test). The excretion rates of both *U. major* and *C. japonica* were also negatively correlated with body size (dry wt) (Fig. 3). The respiration : ammonium excretion ratios (O/N; by atoms) for both species were calculated in Table 1. The O:N ratio of *U. major* was 20.2 ± 8.8 . On the other hand, that of *C. japonica* was high and showed wide variation (47.9 ± 38.5).

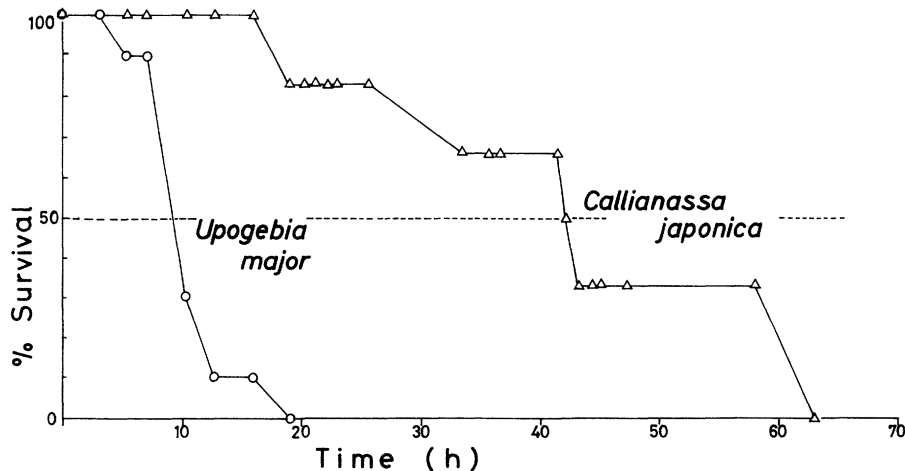


Fig. 6. Survival of *Upogebia major* and *Callianassa japonica* in anoxic sea water; broken line, LD_{50} .

Response to Hypoxic Sea Water

Respiration rates in both species were affected by changes in the dissolved oxygen concentration of the sea water (Fig. 4). In *Upogebia*, reduction in dissolved oxygen (DO) depressed the respiration rate linearly from 100% to 30% of DO saturation; at the 10% saturation level, the average reduction was 53% of the rate in oxygen-saturated sea water. In *Callianassa* no significant effect of hypoxic sea water was found on reduction from the 100% to 30% levels of DO saturation ($P > 0.3$; Student's t-test). Only at 10% oxygen saturation did the respiration rate decrease by 60% (the difference is significant, $P < 0.01$; Student's t-test).

The effects of hypoxic conditions on the rate of ammonium excretion also differed in these two species, as in the case of respiration (Fig. 5). In *Upogebia* there was a significant decrease in the excretion rate when DO concentration fell to 50% of saturation, but in *Callianassa* there was practically no significant change in the rate of ammonium excretion in the DO range from 100% to 10% ($P > 0.3$; Student's t-test). With change of dissolved oxygen concentration, the O:N ratios of these two species showed no significant change. Thus, under reduced oxygen conditions, the O:N ratio of *C. japonica* was also significantly higher than that of *U. major*.

Tolerance of Anoxic Conditions

Under anoxic conditions, both species could survive more than several hours (Fig. 6). The first mortality of *Upogebia* occurred after 5 h of anoxia, and that of *Callianassa* after 19 h. Maximum survival was <19 h for *Upogebia* and <63 h for *Callianassa* (Fig. 6). *Callianassa japonica* ($LD_{50} = 40$ h) was more tolerant of anoxia than *Upogebia major* ($LD_{50} = 9$ h).

DISCUSSION

Digging behavior and burrow morphology of *Upogebia major* and *Callianassa japonica* were almost the same as in other species of *Upogebia* and *Callianassa*, i.e., *U. affinis*, *U. pugettensis*, *U. litoralis*, *C. californiensis*, and *C. stebbingi* (Pearse, 1945; Pohl, 1946; MacGinitie and MacGinitie, 1949; Ott *et al.*, 1976; Swinbanks and Murray, 1981). The feeding habits of burrowing shrimps may influence the form of their burrows, as suggested by L. Thompson and Pritchard (1969) and Swinbanks and Murray (1981) for *C. californiensis* and *U. pugettensis*. In *C. japonica*, continual digging is necessary not only for constructing a burrow as a shelter, but also for feeding. Thus, the shape of burrow is frequently changed. A crater made around the entrance of the burrow is a result of digging the burrow and feeding. On the other hand, *U. major* is a filter-feeder, and a water current is needed both for respiration and feeding. The two wide openings of its burrow are suitable for such irrigation.

It is known that respiration rhythms are related to diurnal and tidal cycles in some marine crustaceans (Wolvekamp and Waterman, 1960). The respiration rates of *U. major* and *C. japonica* fluctuated to some extent even under constant dark conditions during 35–40 h of continuous observation. However, because no consistent rhythm was found, we consider that the results are comparable despite the different diel times of these experiments.

Respiration rates of *U. major* are $0.93 \text{ ml O}_2 \text{ g dry wt}^{-1} \text{ h}^{-1}$ on the average, higher than that of *C. japonica* (average 0.52). Rates of ammonium excretion were also higher in *U. major*, although only a limited amount of data were available (Fig. 4). R. Thompson and Pritchard (1969) also reported significantly higher rates

of respiration in *U. pugettensis* compared to that in *C. californiensis* under oxygen-saturated conditions.

Metabolic activities, such as respiration and excretion, are affected by environmental conditions as well as by the genetic characteristics of each species. *C. japonica* can regulate their metabolic activities, showing oxygen-independent respiration rates above 30% of saturation level. Critical oxygen tension (Prosser, 1955) is between 30–10% of oxygen saturation in this species. In *U. major*, on the other hand, respiration rates are oxygen-dependent from 100% to 30% of oxygen-saturation levels. R. Thompson and Pritchard (1969) reported a similar difference in a critical oxygen tension between two genera (*C. californiensis* and *U. pugettensis*). Similar trends are also observed in the rate of ammonium excretion (Fig. 5). *C. japonica* has more adaptability to low oxygen stress than *U. major*. This is also true for survival under anoxia, an important physiological characteristic for mud shrimps living on intertidal mud flats. In *U. major*, the average of 9-h survival under anoxic conditions was shorter than the time span of maximum exposure which, at the mean sea level, should occur at neap tide because of inequality of two tides in a day. The maximum exposure is expected about 15–16 h in Yamada Bay. Even during exposure, however, dissolved oxygen content in the burrow of *U. major* was maintained at approximately 10% of saturation, suggesting that the shrimp introduces oxygen from the air to its burrow water by activating its pleopods (Koike and Mukai, 1983).

The LD₅₀ of *C. japonica* under anoxia (40 h) was several times longer than that of *U. major* (Fig. 6). An LD₅₀ of 80 h was found by Felder (1979) for *C. jamaicensis* under anoxic conditions. He obtained a slightly longer time, approximately 100 h, by changing the anoxic sea water daily, so that it was free from the influence of accumulated metabolic wastes. Thus the accumulation of metabolic wastes may be one factor determining the length of survival under anoxia. A shorter time, however, would be expected for an *in situ* environment, because the animals cannot exchange their burrow water during low tide. The observation that lactate accumulation in hemolymph of *U. pugettensis* under anoxia was more than 7 times that of *C. californiensis* (Pritchard and Eddy, 1979) confirms the generic difference in adaptabilities for anoxic conditions.

The significant difference in respiration : ammonium excretion rate (O/N) in these two shrimps is of particular interest, since this difference is correlated with the carbon and nitrogen metabolism of the shrimps. As mentioned above, *Callinassa* feeds on sediment particles, while *Upogebia* feeds on suspended particles. The nutritional values of available carbon : nitrogen ratios of these foods are still not well understood. However, if we assume that suspended particles are more

Table 2. Comparison of the physiological and behavioral characteristics of *Upogebia major* and *Callinassa japonica*. Data represent mean values.

	<i>U. major</i>	<i>C. japonica</i>
Texture of sediment in habitat	Sand or muddy sand	Mud or sandy mud
Burrow	Simple Y-shaped	Complex
Feeding	Suspension feeder	Deposit feeder
Respiration rate (ml O ₂ g ⁻¹ h ⁻¹)	0.97	0.43
Response to hypoxic water	Oxyconformer	Oxyregulator
Tolerance to anoxia (LD ₅₀)	9 h	40 h
Ammonium excretion rate (μg-atomsN g ⁻¹ h ⁻¹)	3.81	0.82
O:N ratio (atom : atom)	20.2	47.9

nutritional than the sediment particles, our observations (O/N = 20.2 for *Upogebia* and O/N = 47.9 for *Callianassa*) are consistent with this assumption.

The physiological and behavioral characteristics of *U. major* and *C. japonica* are summarized in Table 2. Although R. Thompson and Pritchard (1969) and Swinbanks and Murray (1981) reported that *Upogebia pugettensis* was found in coarse sediments and *Callianassa californiensis* in muddy sediment, our preliminary observations on the species examined here showed opposite results for the two genera. That is, most *U. major* usually live in sandy sediment, while *C. japonica* lives both in sandy and muddy (anoxic) sediment in Yamada Bay. Dissolved oxygen content in the burrows of *U. major* (average $37 \pm 4\%$ of oxygen saturation) was higher than that in burrows of *C. japonica* (average $23 \pm 15\%$ of oxygen saturation) (Koike and Mukai, 1983). These environmental and ecological observations are consistent with the above arguments concerning behavioral and physiological differences between the two mud shrimps.

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BOOK REVIEW

Debelius, Helmut. 1983. *Gepanzerte Meeresritter*.—Alfred Kernen Verlag, Zweigniederlassung der Reimar Hobbing GmbH, Postfach 10 20 43, Husmannshofstrasse 10, D-4300 Essen 1, Federal Republic of Germany.

This paperback of 120 pages, written in German with a title that may be translated as “Sea Knights in Armor,” contains 86 excellent photographs in color of various living decapod crustaceans (*Stenopus*, *Stenorhynchus*, *Enoplometopus*, *Dardanus*, *Hymenocera*, *Saron*, *Rhynchocinetes*, *Neopetrolisthes*, *Periclimenes*, *Lybia*, and *Lysmata*) as seen in their natural habitats. Observations on living animals are reported and the transportation of the crustaceans and methods of maintenance in aquaria are discussed.

In an appendix a new species, *Saron inermis*, is very briefly described by Ken-ichi Hayashi, with colored photographs of both male and female.

Many picture books lack scientific names for the animals photographed, but in this book the crustaceans have been identified by specialists. Moreover, specimens of most of the crustaceans have been placed for reference in the Senckenberg Museum in Frankfurt.

This book will be interesting and useful to scientific workers and to all interested in the natural history of crustaceans, both lay and professional.—Arthur G. Humes, Boston University Marine Program, Marine Biological Laboratory, Woods Hole, Massachusetts 02543.