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Relationships between Environmental Factors and Diel and Annual Changes of the Behaviors during Low Tides in *Periophthalmus modestus*

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ABSTRACT—The mudskipper, *Periophthalmus modestus*, inhabits the intertidal zone and is active on the surface of mud flat during low tides. We investigated relationships between the behavior and environmental variables during low tides from daily and annual aspects. The observation was done in two distant sites where tidal cycles and population densities are different. The emergence of the mudskipper on the surface of the tidelands was influenced by ambient temperature; low temperature inhibited emergence and locomotor activity of the mudskipper. The mudskipper retreated into the mud as the time went on after emersion of the tideland in order to avoid increase of body temperature and desiccation of the epidermis. Therefore, the emergence of the mudskipper seems to be directly suppressed by drying up of the mud surface. There were no differences in the diel and annual changes in the activity pattern between the populations. The emergence exhibited synodic changes in both areas, and it was correlated not with lunar phase but with tidal amplitude, peaking at the time of lower ebb tides with high air temperature.

INTRODUCTION

The temporal movement of fishes has been well known in nature, and the range of cyclical fluctuation is various from day to year (Wootton, 1990); such as the diel change of foraging in coral reef fishes (Helfman, 1986), semilunar rhythm of spawning (Gibson, 1978) and annual fluctuation of habitat in many fishes. Most of these reports have been discussed from ecological points of view, e.g., prey-predator relationships and synchronization for mating. However, such temporal changes may be affected by not only biotic factors but also environmental conditions directly.

Fishes inhabiting the intertidal zone are exposed to various environmental fluctuations such as photoperiod, temperature, tidal level and so on. Additionally, among intertidal fishes, resident fishes which remain in rockpools or tidelands during low tides are exposed to immersion/emersion alternation of their habitat. Therefore, many studies of biological rhythms of resident fishes have been carried out in respect of adaptation to such complicated and fluctuating environment (Gibson, 1982). Studies of temporal movement in the field in oxudercide gobies, which are one of the large groups in littoral fishes and so-called "mudskipper", have been increasing.

Genus *Periophthalmus* is the most adaptive to terrestrial life among oxudercide gobies (Clayton, 1993), because this group is active to forage and court on the surface of mud flats during low tides in addition to aerial excursion with tides. *Periophthalmus modestus* inhabits the tidelands along Pacific coast from Korea to central Japan (Murdy, 1989) and has been studied well on its ecology and physiology. Ikebe and Oishi (1996) studied in detail the relation between the number in *P. modestus* in air during high tides and environmental parameters, and suggested the adaptive significance of aerial appearance from physiological points of view.

In the present study, we monitored the number of emergent and active fish on the mudflat during low tides in two populations (Uchinoura and Kasaoka) of *P. modestus*. Our purpose is to find out important environmental factors that influence the activity of *P. modestus* in populations living under different temperatures and tidal cycles.

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MATERIALS AND METHODS

Study areas

Field observations on the mudskipper, *Periophthalmus modestus*, were carried out at two sites (Fig. 1a). One is the tideland of Uchinoura Bay, Wakayama Prefecture (33° 41'N, 135° 22'E). The tidal flat in Uchinoura is a small (about 30 m × 50 m) enclosure surrounded by a broadleaf forest. The substratum was very muddy and over one meter in depth, and it is always moist during low tides because of poor drainage. In order to facilitate counting of the number of fish, a quadrat (10 m × 30 m) was provided where the mudskippers were most abundant (Fig. 1b). Another study area, the Kasaoka tideland, is in the outlet of a small stream at Kasaoka Bay, Okayama Prefecture (34° 30'N, 133° 30'E). Although the Kasaoka tideland was relatively large, distribution of the mudskipper was very limited around the center of the mudflat. A quadrat (10 m × 10 m) was set in the area where the fish were most abundant (Fig. 1c). The quadrat was set about 0.5 m high in perpendicular to the tidal channel. Since the soft mud layer in the quadrat was about 80 cm in depth and the lower stratum mainly

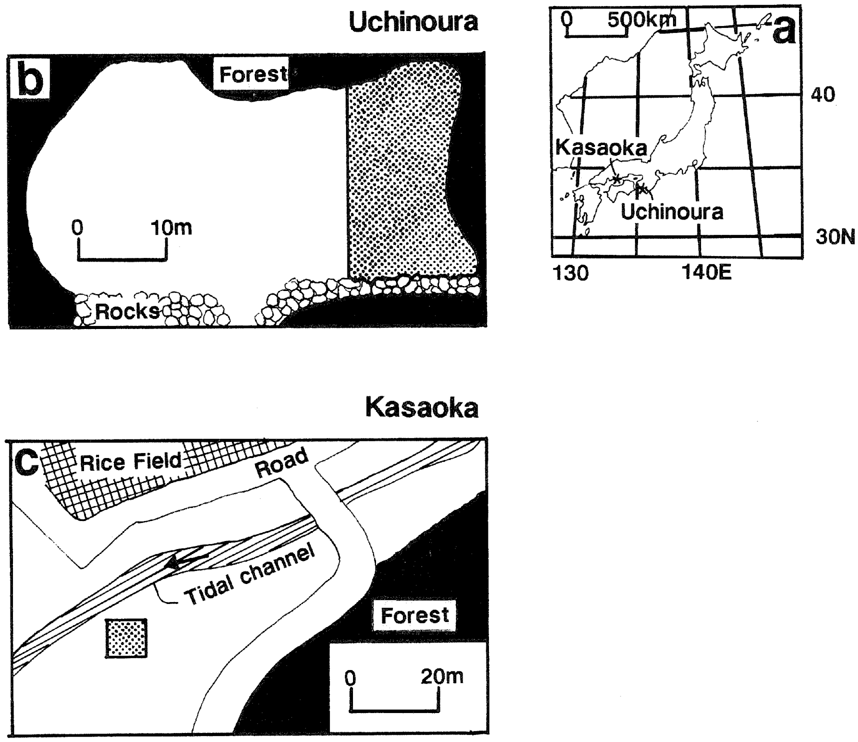

Fig. 1. Location of two study sites in Japan (**a**), and profile of observation sites, Uchinoura (**b**) and Kasaoka (**c**). Dotted areas indicate observation areas.

consisted of sand, the mud surface drained well.

There are differences in population density of the mudskipper and tidal cycles between the Uchinoura and the Kasaoka tidelands. The maximum density within the quadrat in Uchinoura and Kasaoka was $0.16/m^2$ and $2.53/m^2$, respectively. The tidal cycle is about five hours later in Kasaoka than in Uchinoura, e.g., when the time of extreme high tide is at 12:00 in Uchinoura, it is at 17:00 in the same day in Kasaoka.

Counting

We counted the number of mudskippers including active and resting on the surface of mudflat within the quadrat during low tides. Among the emergent fish, the number of crawling fish i.e., foraging, courting fish and those except motionless more than five minutes, was recorded as "locomotor". The counting was carried out with a telescope at a distance not to disturb the behavior of the mudskippers every half an hour in Uchinoura and every hour in Kasaoka. The fish greater than about 30 mm in standard length were countable by this method.

Environmental variables selected were day length, air temperature, tidal level and lunar phase. Air temperature was measured whenever observation was done while the data on the day length, tidal level and lunar phase were obtained from meteorological calendars in Wakayama (1992) and Okayama (1993, 1995).

Observation periods

The Uchinoura population was monitored for 4 days around spring tides from April to November, 1992. In addition, investigation of 22 consecutive days was carried out from 11 June to 1 July. In January, February, March and December of 1992, we investigated whether the mudskipper appeared on the mudflat at spring tides. All counting in Uchinoura was done during the daytime (7:00-18:00).

The Kasaoka population was investigated through more than 2 tidal cycles during spring and neap tides from May to October, 1993. During nocturnal low tides, the counting was performed with the aid of light. In March, April, November and December in 1993, we observed whether the fish appeared on the surface of the mudflat only during the daytime low tides around neap tides. Furthermore, daytime observation (4:00-19:00) of 25 consecutive days was done in summer, from 26 July to 19 August, 1995.

Statistical analysis

Correlations between activity pattern and environmental variables were mainly analyzed by Kendall's rank correlation test. Rayleich test (Zar, 1984) was used to test whether temporal fluctuation has significant periodicity.

RESULTS

Relation between seasonal changes of behavior and those of environmental variables

At the Uchinoura and Kasaoka observation sites, the emergence of the mudskipper showed a distinct seasonal change (Fig. 2). The seasonal change of the behavior can be classified into two periods; the active period during which the fish emerge and forage actively on the mud flat, and the resting period during which the fish stay in their own burrows and cannot be observed on the surface of the mud. For the Uchinoura population, it was mid March that we could find the mudskipper for the first time on the surface of the mudflat. From April to October, many mudskippers appeared on the mud flat and the number declined thereafter. In December, no mudskippers emerged on the surface of the mud. For the Kasaoka population, mudskippers first appeared in April and

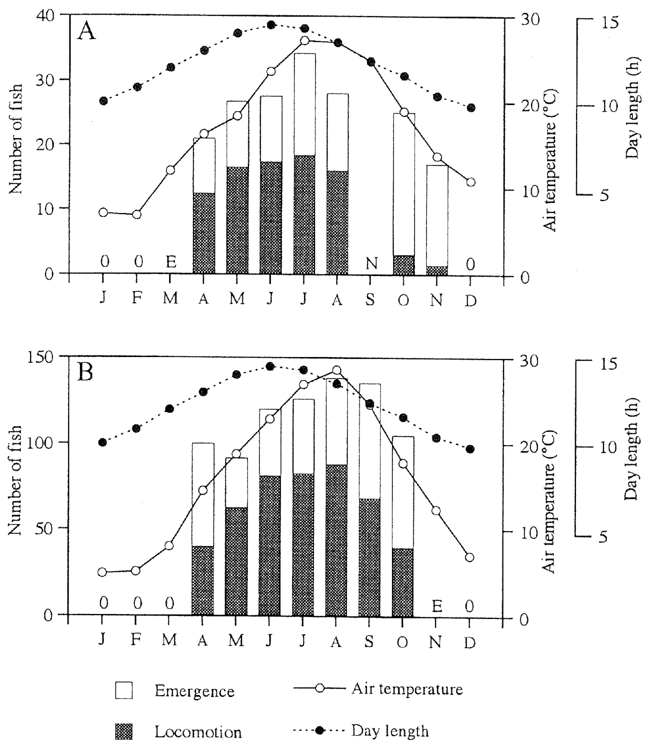

Fig. 2. Annual changes of mean number of emergent and active fish per 100 m². Upper (**A**) and lower (**B**) panels show the Uchinoura and Kasaoka population, respectively. "N" in the upper graph indicates no observation. "E" in the graphs shows that the fish emerged on the surface of the mudflat although the number was not counted. "0" in the graphs shows that none of the mudskippers appeared on the surface of the mudflat when we observed.

were active on the surface of tideland in May. The emergence of fish on the surface of tideland was also observed in April, 1995. The number of emergent fish was kept more than 100 per 100 m² from late June to October in Kasaoka. The number decreased after October, and the fish stayed in the mud from December. In both populations, mudskippers did not emerge on the surface of the mudflat in late November although a few small individuals <30 mm could be observed.

The seasonal change of the locomotor activity on the mud was also great. The mudskippers were active to forage on the tideland in April and May at Uchinoura and Kasaoka, respectively. In summer, the locomotor activity was high and up to fifty percent of the mudskipper emerged were active in both sites. The locomotor activity in the Kasaoka population started to decline after September and most mudskippers were inactive in November. In the Uchinoura population, the locomotor activity became very low after September.

On the annual fluctuation, the number of emergence per an hour was not associated with day length (Kendall's rank correlation test, Z = 0.742, P>0.05), but associated with air temperature (Z = 2.722, P<0.05). Similarly, the mean locomotor activity per an hour was not correlated with day length (Z = 1.732, P>0.05), but correlated with air temperature (Z = 2.227, P<0.05).

The number of emergent fish was correlated with air temperature when the data were pooled in each season (Figs. 3, 4; spring, April-June; summer, July-August; autumn, September-November). In spring and autumn, there was a significant positive correlation, but no significant correlation in summer (Table 1). The number of fish on the mudflat varied widely when air temperature was above 25°C (Figs. 3, 4). The number of emergent fish decreased as the air temperature decreased. The mudskipper did not appear on the surface of tideland below 10°C either in Uchinoura or Kasaoka.

Although air temperature affected not only emergence but also locomotor activity, the response to temperature was different between the two behavior. In the case of Kasaoka population, the regression slopes between the number of locomotion and air temperature were similar in spring and autumn and most of the mudskippers were inactive below 15°C (Fig. 4), although many mudskippers emerged on the mudflat. Similar trends were shown in Uchinoura, and almost all fish

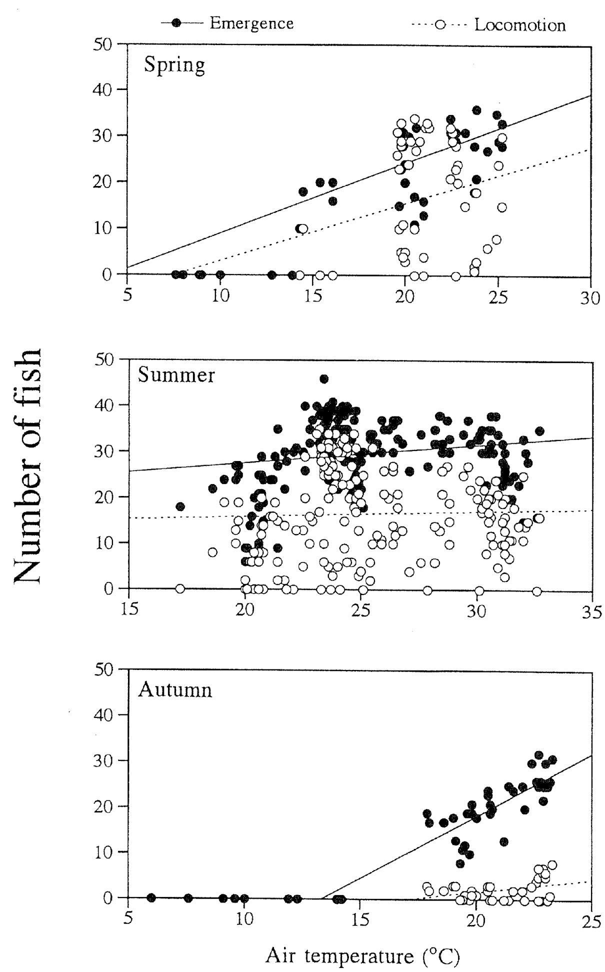

Fig. 3. Relation between the numbers of emergent and active fish and air temperature in each season at Uchinoura. Solid and broken lines indicate regression of the number of emergent and active fish, respectively.

Table 1. Seasonal fluctuation of correlation coefficient (r) between each behavior and air temperature in two different populations

Season	Uchinoura 1992			Kasaoka 1993		
	Emergence	Locomotion	(N)	Emergence	Locomotion	(N)
Spring	0.532*	0.267	(48)	0.406*	0.437*	(53)
Summer	0.195	0.042	(120)	0.220	0.153	(63)
Autumn	0.761*	0.402*	(35)	0.608*	0.722*	(33)

(*; p<0.05)

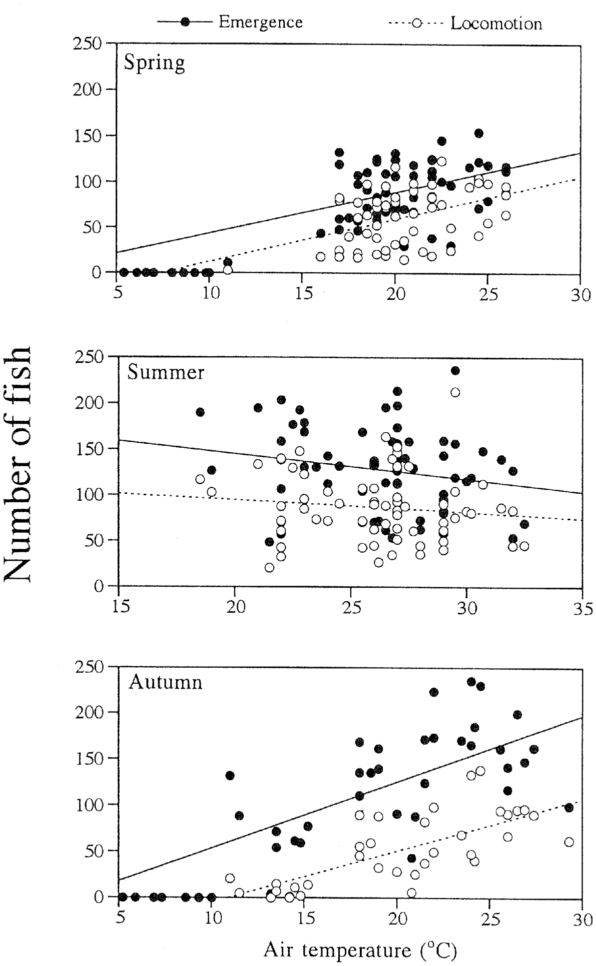

Fig. 4. Relation between the numbers of emergent and active fish and air temperature in each season at Kasaoka. Circles and lines are the same as those in Fig. 3.

emerged were inactive in autumn when temperature was around 20°C (Fig. 3).

Relation between diel changes of emergence and those of environmental factors

On daily fluctuation, the correlation was weak between the number of emergent fish and air temperature at both observation sites; the numbers of days in which the correlation was statistically significant (Kendall's test, $P<0.05$) in Uchinoura and Kasaoka were 2 (7.14%) out of 28 and 6 (20.69%) out of 29, respectively. The number of emergent fish was maximum just after emersion of the mudflat and declined in the course of time, showing an inverse correlation to the time after emersion of tideland. The numbers of days with statistical significance between the number of emergence and the time after tideland emersion were 11 (39.29%) in Uchinoura and 16 (55.17%) in Kasaoka, respectively (Table 2). The number of significant days changed seasonally, and was the largest in summer. In summer of 1995 in Kasaoka, when the air temperature was higher than that in 1993, the significant days were 14 (63.64%) out of 22, and the trend of decline was very clear (Fig. 5). The trend of decline became most distinct when the tideland was exposed to air from 10:00 to 16:00 above 30°C of air temperature. Few mudskippers were observed on the mud just before the tide advances. On the other hand, the slopes of the decrease were not steep in the early morning or at dusk. The number of active fish, similar to emergence, was also found to reduce in the course of time. The statistically significant days were 11 (39.29%) in Uchinoura and 9 (31.03%) in Kasaoka, and there was no difference between each population. The locomotor activity as well as emergence was correlated weakly with air temperature.

Synodic changes of emergence

The change of the maximum number of emergence in observed days was shown in Fig. 6. In the Uchinoura population, the number of emergence showed a semilunar rhythm with a peak at spring tides; sinusoidal curve fit by least square method revealed that the peak was 2 days after the full or new moon. However, the number of emergent mudskipper in 15 June (full moon) declined because of heavy rain. The change of the number of the mudskipper emerged in Kasaoka in 1995 showed similar synodic rhythmicity to the Uchinoura population, although there was a slight phase difference with peaks at 3 days before the full or new moon. These rhythms had a significant periodic component of 15 days ($P<0.01$, Rayleich test). The maximum number of emergence in Uchinoura showed a significant inverse correlation with the lowest tidal level at ebb tide ($Z = -2.22$, $P<0.05$). In the Kasaoka population, the number of emergent fish was also significantly correlated with the lowest tidal level ($Z = -2.19$, $P<0.05$), but not with the lunar phase ($Z = -1.59$, $P>0.1$).

Table 2. Results of correlation test between the number of emergent mudskippers and the course of time after the tideland emerged

Season	Uchinoura 1992		(N)	Kasaoka 1993		(N)
Spring	1 (16.7%)	] *	(6)	3 (37.5%)	] *	(8)
Summer	10 (55.6%)	] *	(18)	11 (78.6%)	] *	(14)
Autumn	0 (0%)		(4)	2 (28.6%)		(7)

Numerals indicate the number of days in which Kendall's rank correlation was significant ($P<0.05$). (*; Binomial test, $p<0.05$)

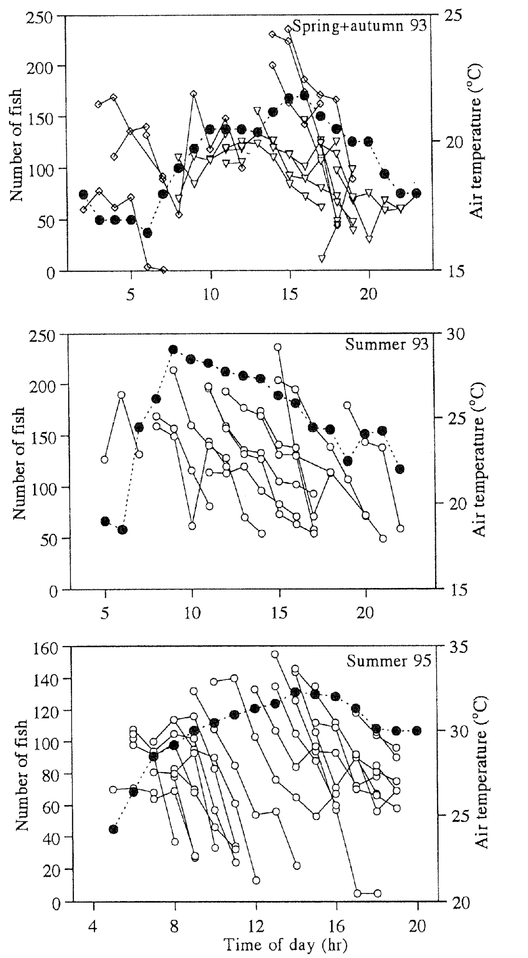

Fig. 5. Fluctuation of the number of emergence during ebb tides in each season at Kasaoka. Triangles and squares indicate the number of emergent mudskippers in spring and autumn (top panel). Open circles show the number of emergence in summer (middle and bottom panels). Solid circles show the mean air temperature per an hour. A group of marks connected with a solid line shows the change of the number of emergent fish during the emersion of the tideland.

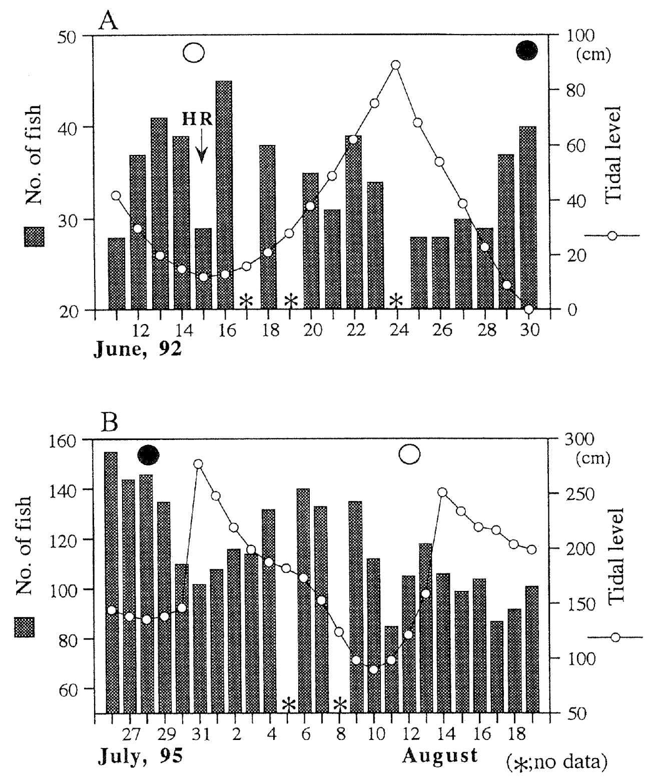

Fig. 6. Synodic changes of the number of emergence. Upper (**A**) and lower (**B**) panels show the Uchinoura and Kasaoka population, respectively. Large open circles and solid ones indicate full and new moon, respectively. HR: heavy rain.

DISCUSSION

It has been known that the behavior of the mudskipper, *Periophthalmus modestus*, shows a distinct annual change (Dotsu and Matoba, 1977). The present investigation confirmed this in two populations under different tidal cycles, Uchinoura and Kasaoka. The start of active period was mid-March in the Ariake (Matoba and Dotsu, 1977) and the Uchinoura populations, while it was in April in the Kasaoka population. It was reported that many *P. modestus* emerged on the tideland above 10°C of air temperature in the Ariake population (Kobayashi *et al.*, 1971). The present study also showed the same trend in the two populations (Figs. 3, 4) and further revealed that the number of emergent fish increased as air temperature became higher, suggesting a direct influence of ambient temperature on emergence. Another species, *P. koelreuteri* in Kuwait Bay was also reported to emerge around 10°C of the mud surface temperature (Tytler and Vaughan, 1983).

The end of active period was late November in both populations in the present study, while the fish stayed in the hole of the mud after mid-November in the Ariake population

(Kobayashi *et al.*, 1971). Thus, the difference may be attributed to difference in temperatures in the two areas, or the susceptibility to temperature or other factors, e.g., reduction of day length.

The locomotor activity on the mudflat was more sensitive to low temperature as compared with emergence. In water-temperature preference experiments of this species (Gordon *et al.*, 1985), the fish chose a warm water (around 30°C) chamber and many fish could no longer move at 10°C. Thus, temperature above 15°C may be necessary for the mudskipper to move actively on the mud flat. Many fish were inactive on the tidal flat below 20°C in autumn even though they emerged. This is similar to basking in juveniles of *B. boddearti* in lower temperature (Tytler and Vaughan, 1983). Although the emergence and locomotor activity increased as temperature rose, the correlation between the activity and temperature became weak under high temperature above 30°C. The numbers of emergent and locomotory fish seem to reach maximum at about 25°C. Since courting males were active regardless of the change of air temperature (unpubl. data), this might also contribute to the weak correlation in summer.

The reduction of the number of fish on the mudflat as the time went on was not caused by migration to outside of the quadrat. We observed that the fish frequently entered into small tide pools during low tides. However, when tide pools on the mud flat disappeared as the time went on, the mudskippers entered the hole in the mud. Gordon *et al.* (1978) reported that *P. cantonensis* (=*P. modestus*) was rarely out of contact with water for more than one minute on sunny days. *P. sobrinus* in Kenya was also observed to take refuge in the nest so as to avoid desiccation at diurnal high temperature (Colombini *et al.*, 1995). Thus, it is suggested that taking refuge in the nest is to avoid the desiccation of epidermis for cutaneous respiration. It is plausible from the fact that the decline of emergence was more distinct in summer than in other seasons and in the afternoon than in the morning (Fig. 5). The Uchinoura tideland easily became shady because of the surrounding copse wood, and water was held well in the mud in comparison with the Kasaoka tideland. Therefore, the number of days with decline of emergence in Kasaoka was greater than that in Uchinoura, supporting the idea that the mudskipper avoids high temperature and/or the desiccation of the skin.

In our investigation, the maximum value of population density was $0.16/m^2$ and $2.53/m^2$ in Uchinoura and Kasaoka, respectively, and the density fluctuated along tidal cycles. Similarly, the population density of *P. modestus* in Korea was extended from $0.5/m^2$ to $2.6/m^2$ (Ryu and Lee, 1979). The trend of diurnal and annual changes of the activity was not different between the two populations despite the fact that the density was 15 times greater in Kasaoka than in Uchinoura.

The pattern of the mudskipper emerged showed synodic periodicity although the phase of fluctuation was different between two observation sites, Uchinoura and Kasaoka. The phase of emergent pattern was correlated not with lunar phase but with tidal amplitude (Fig. 6). It is important that emersion of mudflat occurs near noon with high temperature, i.e., period when the mudflat is most suitable for the mudskippers to be active. Since the emergence of the mudskipper mainly synchronizes to tidal cycles, being affected by temperature at the same time, the pattern of emergence might be expressed in such semimonthly rhythmicity with an inverse relation to tidal amplitudes.

P. modestus and *Boleophthalmus pectinirostris*, which is sympatric with *P. modestus* in the Ariake sound, showed circatidal rhythms under constant condition and such rhythms persist for up to 50 days (Ishibashi, 1973; Nishikawa and Ishibashi, 1975). In addition, Ishibashi (1973) reported that *B. pectinirostris* showed a semilunar rhythm in the amplitude of activity in the laboratory. He considered that the interaction between circadian and circa tidal components induced the semilunar rhythm. The Kenya population of *P. sobrinus* indicated the marked difference of emergent fish in the mudflat between spring and neap tides (Colombini *et al.*, 1995). In Kenya mangrove, where *P. sobrinus* was observed, the degree of emersion of the mudflat was changed by tidal height because of slight inclination of the substratum. Thus, Colombini *et al.* (1995) suggested that the difference of the number of emergent fish was caused by difference of behavior pattern such as zonation between spring and neap tides. On the other hand, since the difference of tidal height between high and low tides is more than 2 m even at neap tides at Kasaoka Bay, the observation site where the quadrat was set, always submerges at high tides and has no difference in the range of emerging area of the tideland between spring and neap tides. Thus, the fluctuation of the number of emergent fish in *P. modestus* is not caused by the difference of distribution due to tidal changes.

Semimonthly periodicity of emergence in the mudskipper is disturbed easily by heavy rain and dryness of mudflat. As previous reports in regard to semilunar rhythms, there are periodicity of spawning of some subtidal fishes (Gibson, 1978), larval release in estuarine crabs (Morgan and Christy, 1994). The feature of these rhythmicity is stable because such rhythms were expressed clearly synchronizing to environmental cycles in spite of bad weather. Synodic rhythmicity of spawning in estuarine crabs can be reproduced in the laboratory if given an appropriate condition (Saigusa, 1986). The ovigerous females must respond faithfully to environmental cycles for the survival of larvae. On the other hand, it may be likely that the rhythmicities of emergence and locomotion are more flexible than that of reproduction. The behavior of the mudskipper in the present study showed plastic rhythmicity under complex environments, which probably has an adaptive significance for survival of individuals.

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