Contents lists available at ScienceDirect

# Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss



# The role of crabs (*Macrophthalmus japonicus*) burrows on organic carbon cycle in estuarine tidal flat, Japan

Sosuke Otani <sup>a,\*</sup>, Yasunori Kozuki <sup>b</sup>, Ryoichi Yamanaka <sup>b</sup>, Hiromitsu Sasaoka <sup>c</sup>, Tetsu Ishiyama <sup>c</sup>, Yoshihito Okitsu <sup>c</sup>, Hajime Sakai <sup>c</sup>, Yoji Fujiki <sup>c</sup>

- <sup>a</sup> Department of Ecosystem Engineering, Graduate School of Engineering, The University of Tokushima, 2-1 Minamijosanjima-cho, Tokushima 770-8506, Japan
- <sup>b</sup> Ecosystem Design, Institute Technology and Science, The University of Tokushima, 2-1 Minamijosanjima-cho, Tokushima 770-8506, Japan
- <sup>c</sup> Department of Ecosystem Engineering, College of Earth and Life Environmental Engineering, Graduate School of Advanced Technology and Science, The University of Tokushima, 2-1 Minamijosanjima-cho, Tokushima 770-8506, Japan

#### ARTICLE INFO

Article history: Received 31 January 2009 Accepted 28 July 2009 Available online 6 August 2009

Keywords: Macrophthalmus japonicus burrows respiration organic carbon cycle

#### ABSTRACT

The objective of this study is to elucidate the burrow structure and to clarify the role of burrows in material cycle in the tidal flat. In our work, we focused on the dominant species in muddy tidal flat, crab *Macrophthalmus japonicus*.

Burrow structure of *Macrophthalmus japonicus* was investigated on a Katsuura river tidal flat in Tokushima prefecture, Japan, using *in situ* resin casting. Sampling was conducted in August 2006, and a total of 48 burrow casts were obtained. Burrows consisted mainly of J-shaped structures (98%) while the rest belonged to U-shaped structures (2%). The maximum measured burrow volume was 120 cm $^3$  and wall surface area was 224 cm $^2$ , while maximum burrow length and depth were 23.2 cm and 16.5 cm, respectively. Burrow volume and surface area were strongly correlated with carapace width of *M. japonicus*. Investigation of the individual number of *M. japonicus* in 13 quadrats (50 × 50 × 20 cm) was conducted using 2 mm sieve. The number of *M. japonicus* was 15–31 ind./m $^2$ . Using cohort analysis we estimated that surface area of burrows was 0.07–0.15 m $^2$ /m $^2$ .

 $CO_2$  emission rate was measured at the surface sediment during the period from June to December 2008. Results varied from  $13.8 \pm 2.2$  to  $49.4 \pm 3.2$  mg  $CO_2/m^2/h$ , and organic carbon decomposition was  $3.8 \pm 0.6$ – $13.5 \pm 0.9$  mg  $C/m^2/h$ . This leads the increase of organic carbon decomposition by 1.1 times, because of the expansion of the tidal flat surface area by burrowing activity. Organic carbon decomposition in burrow walls therefore contributed to organic matter decomposition in the tidal flat. These results indicated that *in situ* activities of *Macrophthalmus japonicus* significantly influence the material cycle and it is important to consider the existence of burrow in order to understand the fluxes of materials and to evaluate the purification function of the tidal flat.

© 2009 Elsevier Ltd. All rights reserved.

#### 1. Introduction

Intertidal areas of estuaries are productive and dynamic systems with extreme and variable environmental conditions (Heip et al., 1995). They are functionally connected to adjoining coastal waters via advective transfers of water and dissolved, particulate material, and ecological food chain of macrobenthos. These interactions are fundamental to understand the roles that estuaries play in the functioning of coastal waters. Especially, organic matter is a major component of estuarine sediments, one of the most important food

sources and organic matter decomposition occurs mainly in sediments (Nedwell et al., 1999). Moreover, rates and pathways of carbon flux have been measured infrequently in tropical coastal sediments (Taylor and Allanson, 1995; Middelburg et al., 1996; Alongi et al., 1999).

Macrobenthos are common in tidal flat and play an important role in purification functions. Organic matter decomposition in sediments may be mediated by the activity of macrobenthos (Herman et al., 1999). They can affect sediments chemistry by bioturbation such as burrow activity, tube-building, ingestion, defecation, respiration and mucus secretion (e.g. Kostka et al., 2002). Therefore, the influence of bioturbation on material cycle in tidal flat caused by their living activities cannot be ignored. The purification functions of Nereidae and Bivalvia, which are the macrobenthos have been intensively studied (e.g. Jordan and

<sup>\*</sup> Correspondence author at: Research Center for Environmental Quality Management, Kyoto University, 1-2 Yumihama, Otsu, Shiga 520-0811, Japan. E-mail address: otani@biwa.eqc.kyoto-u.ac.jp (S. Otani).

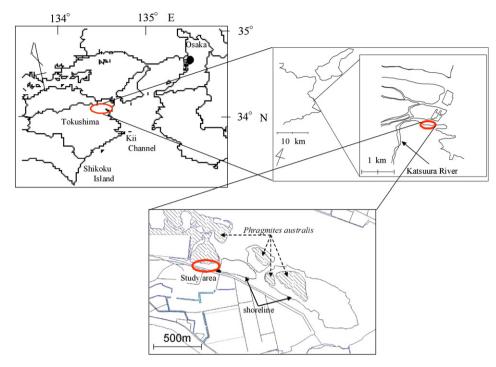


Fig. 1. Study area.

Valiela, 1982; Yamamuro and Koike, 1994) in earlier studies. It is well known that some crabs reduce carbon and nutrient exports from mangrove forests by actively burying litter within their burrows (Robertson, 1986; Twilley et al., 1997), in addition, it was reported that mangrove crabs are ecosystem engineers (Kristensen, 2008). However, Ocypodids have been hardly detail studied regarding the material cycle in tidal flat, although the species is abundant.

We focused on the crab *Macrophthalmus japonicus*, which is distributed widely and dominantly in Japan (Kitaura et al., 2002). The crab, relatively large (up to 35 mm carapace width) and one of the most abundant macrobenthos, is also a burrowing species that inhabit muddy tidal flats. In previous studies, it has been observed that reproduction (Henmi and Kaneto, 1992; Henmi, 1992b), lifehistory (Henmi, 1989, 1992c), wandering (Henmi, 1992a) of *M. japonicas*. Although these biologies have been revealed, crab bioturbation is expected to affect material cycle in tidal flat. We speculated that the burrowing activities play an important role in the purification function in the tidal flat. Furthermore, indirect

effects of bioturbation such as burrowing activity should be considered to evaluate purification in tidal flat, as well as direct effects of production and consumption of macrobenthos.

The objectives of this study are to elucidate the burrow structure and to clarify the role of burrows in material cycle in the tidal flat.

#### 2. Material and methods

Katsuura River (34°02′N, 134°34′E) is located in the eastern part of Shikoku Island, in west Japan (Fig. 1). Our field investigation was carried out on a muddy tidal flat which is about 0.5 ha of whole 9 ha, from the river mouth to about 2 km upstream. The muddy tidal flat lies the reed, *Phragmites australis*, grows thickly around it. The sediment of the muddy tidal flat consists of mud containing about 50% silty clay.

Quadrat  $(50 \times 50 \times 20 \text{ cm})$  samples of *Macrophthalmus japonicus* were collected to examine the abundance using 2 mm mesh sieve at 13 stations during the period from June to December 2008. The carapace width of *M. japonicus* was measured using calipers.

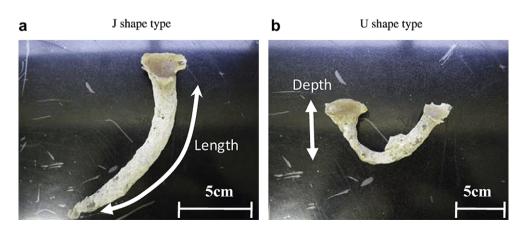


Fig. 2. Typical burrow casts.

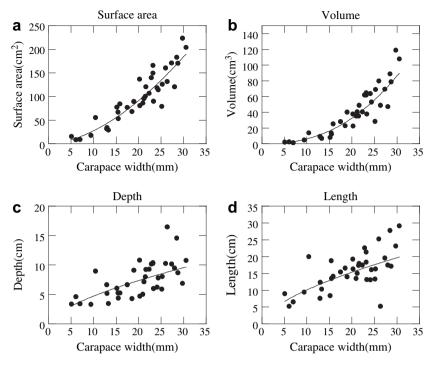


Fig. 3. Relationships of carapace width with burrow measurements.

The carapace width–frequency data from *M. japonicus* were analyzed using PROGEAN VER.4.0J (Tsutsumi and Tanaka, 1994). Cohort analysis was performed with the frequency distribution of carapace width for secondary production. Sediment samples down to 4 cm were collected by using an acrylic core tube (15 mm in diameter) which was measured top 5 mm surface sediment Chl. *a* at 6 stations. Chl. *a* was measured as Whitney and Darley (1979), and primary production of *Nitzschia* sp. was estimated by Montani et al. (2003).

We investigated burrows of *Macrophthalmus japonicus* to elucidate its burrow structure. Burrow casts were obtained in August 2006, using polyester resin (Eporak G-226P and G-226PS, Nihon Shokubai) as Kinoshita (2002). Liquid resin was poured in frames that covered several burrows. About 24 h later, resin casts were pulled out and recovered. In the laboratory, burrows' depth and length were measured directly resin casts using measure. Surface area was calculated by Scion Image (Scion Corp.) covered aluminum foil with resin casts. Volume was detected water volume spilled out from container into resin casts.

Two ways of experiments were performed to quantify respiration rate of *Macrophthalmus japonicus* in ebb and flood tide. We demonstrated that oxygen consumption of *M. japonicus* in the air ( $O_2$ UP TESTER, TAITEC). This equipment measured only oxygen consumption, with sodium hydroxide absorbed  $CO_2$  which *M. japonicus* respired. Two experiments were conducted on same individuals and under the condition, with sodium hydroxide and without it. Hence, it was measured that only oxygen consumption with sodium hydroxide, and oxygen consumption plus carbon dioxide without sodium hydroxide in order to estimate carbon dioxide from two experiments. The experiment was conducted under the  $20\,^{\circ}$ C (spring),  $30\,^{\circ}$ C (summer),  $20\,^{\circ}$ C (fall),  $10\,^{\circ}$ C (winter) in air temperature. After 24 h starvation period in the laboratory, crabs were acclimated to the equipment for 2 h.

We demonstrated that oxygen consumption of *Macrophthalmus japonicus* in the water. After 24 h starvation period in the laboratory, crabs were acclimated to the flasks (370 mL) in the seawater for 2 h to reduce stress, and afterwards a water sample was exchanged to

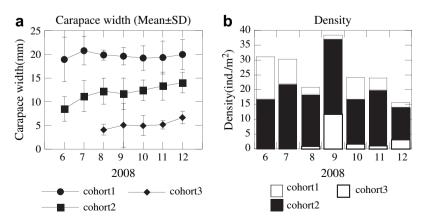


Fig. 4. Results of cohort analysis.

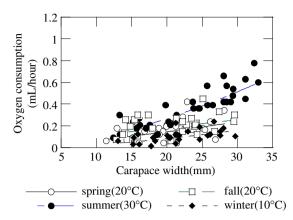


Fig. 5. Oxygen consumption of M. japonicus in the air.

saturated sterilization filtration seawater to determine the initial concentration of oxygen (DO21-P, TOA-DDK). Later, flasks were sealed for 1 h, after measuring final concentrations. One flask without a crab for each treatment was added as a control. The experiment was conducted under 30, 20, 10 °C in water temperature.

We conducted measurements of  $CO_2$  emission rate from the surface sediment in the field during the ebb tide to examine the organic matter decomposition rates. In situ  $CO_2$  emission rate from the surface sediment was measured using  $CO_2$  sensor (Telaire 7001, Onset) placed in an acrylic chamber ( $\emptyset$ : 9 cm, height: 20 cm) from June to December 2008. We carefully detected that 5 min measuring  $CO_2$  emission rate after the value was stable condition. Because temperature rises inside the chamber in summer, we surrounded around the chamber with the ice pack to suppress temperature rise.

# 3. Result

#### 3.1. Burrow structure

A total of 48 burrow casts were obtained. Structurally, the burrows consisted of J shape type and U shape type. 98% of the burrows were J type and 2% of the burrows were U type (Fig. 2).

The relationship between carapace width and various burrow parameters is shown in Fig. 3. Burrow surface area ranged from 8.4 to  $224.1~\rm cm^2$  and burrow volume ranged from 1.5 to  $119~\rm cm^3$ , burrow depth ranged from 3.3 to 16.5, burrow length ranged from 5.2 to  $23.2~\rm cm$ , ranging from  $5.05~\rm to$   $30.50~\rm mm$  of carapace width. Formulas to estimate burrow parameters from carapace width (CW, mm) as follow: (1) surface area (cm²) =  $0.505\rm CW^{1.74}$ ,  $R^2 = 0.88$ ; (2) volume (cm³) =  $0.024\rm CW^{2.40}$ ,  $R^2 = 0.90$ ; (3) depth (cm) =  $1.063\rm CW^{0.62}$ ,  $R^2 = 0.44$ ; (4) length (cm) =  $2.274\rm CW^{0.61}$ ,  $R^2 = 0.41$ . In the case of carapace was  $25~\rm mm$ , for instance, it was estimated that surface area was  $136.7~\rm cm^2$  and volume was  $54.4~\rm cm^3$ .

A similar result was obtained that average burrow depth was 10–15 cm and the burrow casts almost consisted of J shape type using plaster (Utashiro, 1966). In addition, it was revealed that there was significant relationship between carapace width and various burrow parameters.

**Table 1**Comparison of oxygen consumption in the air and water.

Temperature (°C)	Oxygen consumption (mLO <sub>2</sub> /h)		
	In the air	In the water	
10	0.11	0.09	
20	0.18	0.21	
30	0.36	0.42	
Ono (1965)	0.33	0.49	

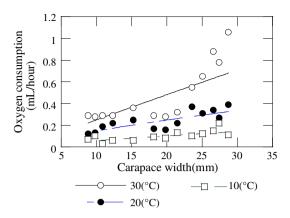


Fig. 6. Oxygen consumption of M. japonicus in the water.

# 3.2. Primary production and secondary production

Chl. a as microphytobenthos biomass in surface sediments (0–0.5 cm) fluctuated 3.0–12.6 mg Chl.  $a/m^2$  and primary production was estimated 1.6–9.1 mg C/m $^2$ /h in this study. Montani et al. (2003) and Colijin and de Jonge (1984) reported that primary production was 33–215 (average: 89.4) and 1–120 (average: 37.0) mg C/m $^2$ /h, respectively, which are higher than in our study.

Fig. 4 indicates results of cohort analysis. Three cohorts were detected during the sampling period. The smallest cohort (cohort 3), which recruited in August 2008 at a mean size of about 4.4 mm, grew to about 6.1 mm by December. The middle cohort (cohort 2) grew to 5.6 mm in 6 months. No apparent growth of cohort 1 was observed. Density fluctuated 15–31 ind./m², and cohort 2 was high in population. It was estimated that secondary production was  $0-1.43 \text{ mg C/m}^2/h$ .

#### 3.3. Respiration rate

# 3.3.1. In the air

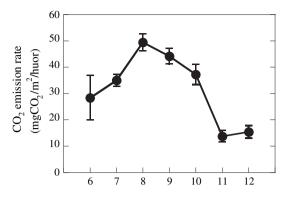
Fig. 5 indicates oxygen consumption of *Macrophthalmus japonicus* in the air. Oxygen consumption of *M. japonicus* increased as the temperature rose. Oxygen consumption in 30 °C and 10 °C was 0.36 and 0.11 mL  $O_2/h$  (Table 1), respectively, and oxygen consumption of *M. japonicus* at 30 °C was 3.3 times higher than that at 10 °C. This is because *M. japonicus* became more active with the temperature rise in the daytime. A significant correlation was recognized between oxygen consumption and carapace width of *M. japonicus* in all season. Formulas for relationships of carapace width (CW, mm) with oxygen consumption (OC, mL  $O_2/h$ ) of *M. japonicus* in the air as follows: (spring, 20 °C) OC = 0.0042CW<sup>1.19</sup>,  $R^2 = 0.24$ ; (summer, 30 °C) OC = 0.022CW<sup>1.60</sup>,  $R^2 = 0.75$ ; (fall, 20 °C) OC = 0.018CW<sup>0.778</sup>,  $R^2 = 0.15$ ; (winter, 10 °C) OC = 0.00060CW<sup>1.64</sup>,  $R^2 = 0.31$ .

# 3.3.2. In the water

Fig. 6 indicates oxygen consumption of *Macrophthalmus japonicus* in the water. Oxygen consumption of *M. japonicus* increased as the temperature rose as in the air. Oxygen consumption in 30 °C and

**Table 2**Comparison of respiration quotient in each season.

Season	Temperature (°C)	Respiration quotient
Spring	20	0.788
Summer	30	0.741
Fall	20	0.781
Winter	10	0.776



**Fig. 7.**  $CO_2$  emission rates (mean  $\pm$  SE).

10 °C is 0.42 and 0.09 mL O<sub>2</sub>/h (Table 1), respectively, and oxygen consumption of *M. japonicus* at 30 °C was 4.7 times higher than that at 10 °C. The values were similar to that of in the water and air, oxygen consumption in 30 °C was similar with Ono (1965) (Table 1). It was reported that oxygen consumption of crab was different in the water and air (Teal, 1959; O'Mahoney and Full, 1984), but there was no difference in oxygen consumption of *M. japonicus* in water and air in this study. Formulas for relationships of carapace width (CW, mm) with oxygen consumption (OC, mL O<sub>2</sub>/h) of *M. japonicus* in the water as follows: (spring and fall, 20 °C) OC = 0.026CW<sup>0.75</sup>,  $R^2$  = 0.65; (summer, 30 °C) OC = 0.028CW<sup>0.95</sup>,  $R^2$  = 0.69; (winter, 10 °C) OC = 0.0082CW<sup>0.84</sup>,  $R^2$  = 0.52.

#### 3.3.3. Respiration auotient

Respiration of *Macrophthalmus japonicus* was also detected in the air, and respiration quotient was estimated from oxygen consumption and  $CO_2$  emission each seasons. Table 2 indicates relationship between oxygen consumption and  $CO_2$  emission in each season. The inclination of the regression line was used as respiratory quotient. Respiration quotient ranged from 0.741 to 0.788, there was no difference observed in each season.

Respiration rate in the population of *Macrophthalmus japonicus* in this tidal flat was presumed. It was converted from oxygen consumption to  $CO_2$  emission with respiration quotient. Seasonal respiration rates were devised as follows: spring (March–May), summer (June–August), fall (September–November), winter (December–February). Respiration rate in the population of *M. japonicus* was calculated from 0.31 to 2.56 g C/m²/month in ebb and flood tide.

# 3.4. CO<sub>2</sub> emission rates

Organic matter decomposition was determined by measuring  $CO_2$  emission rates in organic carbon cycle. Fig. 7 indicates  $CO_2$  emission rates.  $CO_2$  emission rates ranged from 13.8  $\pm$  2.2 to 49.4  $\pm$  3.2 mg  $CO_2/$   $m^2/h$ , and translated to organic carbon decomposition rate was

 $3.8\pm0.6$  to  $13.5\pm0.9$  mg C/m²/h. CO<sub>2</sub> emission rates in this tidal flat showed a slightly low value when compared to next values, 27–35 mg CO<sub>2</sub>/m²/h (Sasaki et al., 2009), 13–26 mg CO<sub>2</sub>/m²/h (Migné et al., 2002), 13–188 mg CO<sub>2</sub>/m²/h (Middelburg et al., 1996), 0.046–2.08 mg C/m²/h (Seiki et al., 1998). A significant statistical correlation was recognized between sediments temperature and CO<sub>2</sub> emission rates (P < 0.01, r = 0.90, n = 7).

# 4. Discussion

Surface area was extended 0.07–0.15 m<sup>2</sup>/m<sup>2</sup> by burrowing of *Macrophthalmus japonicus*. From the result of cohort analysis, we calculated that total burrow surface area increased from 358 to 771 m<sup>2</sup>, which corresponds to 7–15% of this muddy tidal flat area.

Hence, we tried to presume organic carbon cycle in the study area. Organic carbon cycle consists of organic carbon decomposition by bacteria in sediment, the fixation of the organic carbon of secondary production of macrobenthos and primary production of microphytobenthos. In addition, organic carbon decomposition in burrow wall. We defined organic carbon cycle as follows.

$$Y = Sc + Bc + Mc - Mp - Pp$$

*Y*: organic carbon cycle ( $g C/m^2/month$ ), Sc: organic carbon decomposition rates in sediment ( $g C/m^2/month$ ), Bc: organic carbon decomposition rates in burrow ( $g C/m^2/month$ ), Mc: respiration rate ( $g C/m^2/month$ ), Mp: secondary production ( $g C/m^2/month$ ), Pp: primary production ( $g C/m^2/month$ ).

Since a significant difference was not recognized statistically oxygen consumption between organic carbon of sediment of surface (0 cm) and burrow wall (-10 cm) (unpublished data), we assumed that was similar to organic carbon decomposition rates in surface sediment and burrow wall. Moreover, the fixation of the organic carbon was assumed to be 0, when the secondary production of *Macrophthalmus japonicus* indicated a negative value.

Here, it was thought that the organic carbon was not decomposed in ebb tide, because there was little dissolved oxygen in water almost remained in the burrow (Koike and Mukai, 1983; Wolfrath, 1992, unpublished data), and actually area in the burrow wall up to approximately 5 cm in depth was exposed to atmosphere. Therefore, we estimated burrow depth from carapace width of *Macrophthalmus japonicus* and calculated organic carbon decomposition in depth 5 cm in ebb tide. As a result, the surface area to depth 5 cm for the surface area to all depth was 82–98% of the surface area in the burrow. On the contrary, the dissolved oxygen in burrow was recovered when a tidal flat surface was covered with water, it was assumed that organic carbon decomposition by the whole burrow was performed.

Table 3 indicates organic carbon cycle. Organic carbon cycle in July 2008 indicated, for example, organic carbon decomposition rate in sediment was  $7.10 \,\mathrm{g}\,\mathrm{C/m^2/month}$  and organic carbon decomposition rate in burrow was  $0.68 \,\mathrm{g}\,\mathrm{C/m^2/month}$ . In addition,

**Table 3** Organic carbon cycle (g C/m<sup>2</sup>/month).

Mont	h Sediments	Release		Accumulation		Organic carbon	
temperature	temperature (°C)	Organic carbon decomposition rates in sediment	Organic carbon decomposition rates in burrow	Respiration rate	Secondary production	Primary production	cycle
6	26.0	5.76	0.52	2.64	0.00	7.06	1.87
1	27.8	7.10	0.68	2.69	1.03	5.21	4.22
8	30.9	10.03	0.61	1.71	0.07	2.59	9.69
9	29.6	8.68	0.69	1.55	0.00	9.14	1.79
10	23.4	7.56	0.60	1.31	0.13	2.47	6.87
11	18.5	2.72	0.21	1.26	0.20	3.67	0.32
12	12.6	3.03	0.14	0.31	0.20	1.59	1.68

respiration rate was  $2.69 \, {\rm g \, C/m^2/month}$ . The amount of release of organic carbon was  $10.47 \, {\rm g \, C/m^2/month}$ . On the other hand, secondary production was  $1.03 \, {\rm g \, C/m^2/month}$  and primary production was  $5.21 \, {\rm g \, C/m^2/month}$ . It means that organic carbon accumulation was  $6.24 \, {\rm g \, C/m^2/month}$ . In fact, organic carbon was totally released by  $4.22 \, {\rm g \, C/m^2/month}$  in this month.

A significant statistical correlation was recognized between sediments temperature and organic carbon decomposition rate in sediment (P < 0.01, r = 0.90, n = 7) and in burrows (P < 0.01, r = 0.93, n = 7). It was not recognized that a significant statistical correlation between sediments temperature and primary production, secondary production, respiration rate, respectively. There were also not a significant statistical correlation among parameters.

The burrowing activity of Macrophthalmus japonicus increased the surface area of tidal flat and also organic carbon decomposition. This leads the increase of organic carbon decomposition by 1.1 times, because of the expansion of the tidal flat surface area by burrowing activity. Organic carbon decomposition in burrow walls, therefore, burrowing activities increased surface area which contributed to organic carbon decomposition. As for the organic carbon release, contribution by organic carbon decomposition of surface sediment was highest. In deed, respiration rate of M. japonicus was higher than organic carbon decomposition in burrow. However, the effects of removed sediment on the surface sediment after burrowing activity were not included in this calculation such as oxidization of the removed sediment itself and resuspension at the flood tide. Total amount of organic carbon cycle of M. japonicus will increase if these effects would be elucidated. Moreover, it needed to show the date though at least one year, considering temporal and spatial variability in the future.

Earlier studies indicated that macrobenthos contribute to the organic carbon cycle (Dye, 1981; Kikuchi, 1987). However, these researches were conducted only with the organic carbon decomposition of surface sediment and respiration rate of the macrobenthos. In this paper, we considered the organic carbon decomposition of burrow wall and production of the macrobenthos as parameters and analyzed their contribution. In this study area, it was indicated that organic carbon cycle increased about 1.1 times when the existence of Macrophthalmus japonicus was considered. When production and respiration rate were considered in the effect of the bioturbation of burrowing activity such as polychaetes (Kikuchi, 1987) and Helice tridens (Kurihara et al., 1989) as well as M. japonicus, organic carbon cycle on the tidal flat showed increase more than it had been considered. These results indicated that in situ activities of M. japonicus significantly influence the material cycle and it is important to consider the existence of burrow in order to understand the fluxes of materials and to evaluate the purification function of the tidal flat.

### 5. Conclusion

As for the burrow, many of its structure was J-shaped type, and it was recognized statistically significant correlation among carapace width, surface area and volume. It was estimated that tidal flat surface area increased 1.1–1.2 times by burrowing activity which corresponds to 7–15% of this muddy tidal flat area.

Two ways of experiments were performed to quantify respiration rate of *Macrophthalmus japonicus* in water and air. There was no difference in oxygen consumption of *M. japonicus* in water and air. It was also recognized statistically significant correlation between carapace width and oxygen consumption of *M. japonicus* in water and air, respectively. Thus, we could estimate burrow parameters and respiration rate from carapace width.

The organic carbon cycle in the tidal flat increased 1.1 times by considering the existence of *Macrophthalmus japonicus* burrow.

These results indicated that *in situ* activities of *M. japonicus* significantly influence on the organic carbon cycle and it is important to consider indirect effects of bioturbation as burrowing activity and direct effects such as production, consumption of macrobenthos to evaluate the purification function of the tidal flat.

# Acknowledgements

We would also like to thank laboratory member for their supports and guidance throughout this study. This research was supported in part by the River Fund in charge of the Foundation of River and Watershed Environment Management (FOREM), Japan.

#### References

- Alongi, D.M., Tirendi, F., Dixon, P., Trott, L.A., Brunskill, G.J., 1999. Mineralization of organic matter in intertidal sediments of a tropical semi-enclosed delta. Estuarine, Coastal and Shelf Science 48, 451–467.
- Colijin, F., de Jonge, V.N., 1984. Primary production of microphytobenthos in Ems-Dollard estuary. Marine Ecology Progress Series 14, 185–196.
- Dye, A.H., 1981. A study of benthic oxygen consumption on exposed sandy beaches. Estuarine, Coastal and Shelf Science 13, 671–680.
- Heip, C.H.R., Goosen, N.K., Herinan, P.M.J., Kiomkamp, J., Middelburg, J.J., Soetaert, K., 1995. Production and consumption of biological particles in temperate tidal estuaries. Oceanography and Marine Biology: an Annual Review 33 1–149
- Herman, P.M.J., Middelburg, J.J., Van de Koppel, J., Heip, C.H.R., 1999. Nutrients in estuaries. In: Nedwell, D.B., Raffaelli, D.G. (Eds.), Advances in Ecological Research: Estuaries. Academic Press, San Diego, CA, pp. 195–240.
- Henmi, Y., 1992a. Factors influencing drove formation and foraging efficiency in *Macrophthalmus japonicus* (De Haan) (Crustacea: Ocypodidae). Journal of Experimental Marine Biology and Ecology 131, 255–265.
- Henmi, Y., 1992b. Reproductive ecology of three ocypodid crabs II. Incubation sites and egg mortality. Ecological Research 4, 261–269.
- Henmi, Y., 1992c. Annual fluctuation of life-history traits in the mud crab Macrophthalmus japonicus. Marine Biology 113, 569–577.
- Henmi, Y., 1989. Life-history patterns in two forms of *Macrophthalmus japonicus* (Crustacea: Brachyura). Marine Biology 101, 53–60.
- Henmi, Y., Kaneto, M., 1992. Reproductive ecology of three ocypodid crabs I. The influence of activity differences on reproductive traits. Ecological Research 4, 17–20
- Jordan, T.E., Valiela, I., 1982. A nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its significance in nitrogen flow in a New England salt marsh. Limnology and Oceanography 27, 75–90.
- Kikuchi, E., 1987. Effects of the brackish deposit-feeding polychaetes *Notomastus* sp. (Capitellidae) and *Neanthes japonica* (Izuka) (Nereidae) on sedimentary O<sub>2</sub> consumption and CO<sub>2</sub> production rates. Journal of Experimental Marine Biology and Ecology 114, 15–25.
- Kinoshita, K., 2002. Burrow structure of the mud shrimp Upogebia major (Decapoda: Thalassinidea: Upogebiidae). Journal of Crustacean Biology 22 (2), 474–480.
- Kitaura, J., Nishida, M., Wada, K., 2002. Genetic and behavioral diversity in the Macrophthalmus japonicus species complex (Crustacea: Brachyura: Ocypodidae). Marine Biology 140, 1–8.
- Koike, I., Mukai, H., 1983. Oxygen and inorganic nitrogen contents and fluxes in burrows of the shrimps *Callianassa japonica* and *Upogebia major*. Marine Ecology Progress Series 12, 185–190.
- Kostka, J.E., Gribsholt, B., Petrie, E., Dalton, D., Skelton, H., Kristensen, E., 2002. The rates and pathways of carbon oxidation in bioturbated saltmarsh sediments. Limnology and Oceanography 47, 230–240.
- Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. Journal of Sea Research 59, 30–43.
- Kurihara, Y., Hosoda, T., Takeda, S., 1989. Factors affecting the burrowing behaviour of *Helice tridens* (Grapsidae) and *Macrophthalmus japonicus* (Ocypodidae) in an estuary of northeast Japan. Marine Biology 101, 153–157.
- Middelburg, J.J., Klaver, G., Nieuwenhuize, J., Wielemaker, A., De Haas, W., Vlug, T., Van der Nat, J., 1996. Organic matter mineralization in intertidal sediments along an estuarine gradient. Marine Ecology Progress Series 132, 157–168.
- Migné, A., Davoult, D., Spilmont, N., Menu, D., Boucher, G., Gattuso, J.-P., Rybarczyk, H., 2002. A closed-chamber CO<sub>2</sub> flux method for estimating intertidal primary production and respiration under emersed conditions. Marine Biology 140, 865–869.
- Montani, S., Magni, P., Abe, N., 2003. Seasonal and interannual patterns of intertidal microphytobenthos in combination with laboratory and areal production estimates. Marine Ecology Progress Series 249, 79–91.
- Nedwell, D.B., Jickells, T.D., Trimmer, M., Sanders, R., 1999. Nutrients in estuaries. In: Nedwell, D.B., Raffaelli, D.G. (Eds.), Advances in Ecological Research: Estuaries. Academic Press, San Diego, CA, pp. 43–92.
- O'Mahoney, P.J., Full, R.J., 1984. Respiration of crabs in air versus water. Comparative Biochemistry and Physiology 79A, 275–282.

- Ono, Y., 1965. On the ecological distribution of ocypoid crabs in the estuary. The Memoirs of the Faculty of Science, Kyushu University, Series E (Biology) 4 (1), 1–60.
- Robertson, A.I., 1986. Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. Journal of Experimental Marine Biology and Ecology 116, 235–247.
- Sasaki, A., Hagimori, Y., Nakatsubo, Y., Hoshika, A., 2009. Tidal effects on the organic carbon mineralization rate under aerobic conditions in sediments of an intertidal estuary. Ecological Research, 24, pp. 723–729.
- Seiki, T., Hiraoka, K., Lee, J.-G., Nishijima, W., Mukai, T., Takimoto, K., Okada, M., 1998. Study on purification ability for the water quality in tidal flats in Hiroshima Bay: evaluation for the characteristics of organic matter decomposition. Japan Society on Water Environment 21, 421–428.
- Taylor, D.I., Allanson, B.R., 1995. Organic carbon fluxes between a high marsh and estuary, and the inapplicability of the outwelling hypothesis. Marine Ecology Progress Series 120, 263–270.
- Teal, J.M., 1959. Respiration of crabs in Georgia salt marshes and its relation to their ecology. Physiological Zoology 32 (1), 1–14.

- Tsutsumi, H., Tanaka, M., 1994. Cohort analysis of size frequency distribution with computer programs based on a graphic method and Simplex's method. Benthos Research 45, 1–10 (in Japanese with English abstract).
- Twilley, R.R., Pozo, M., Garcia, V.H., Rivera-Monroy, V.H., Bodero, R.Z.A., 1997. Litter dynamics in riverine mangrove forests in the Guayas River estuary, Ecuador. Oecologia 111, 109–122.
- Utashiro, T., 1966. Ecology and burrows of *Macrophthalmus japonicus*: biological studies in Lebensspuren Part 8. Memoirs of Takada Branch, Faculty of Education, Niigata University 11, 131–145 (in Japanese with English abstract).
- Whitney, D.E., Darley, W.M., 1979. A method for the determination of chlorophyll *a* in samples containing degradation products. Limnology and Oceanography 24, 183–186.
- Wolfrath, B., 1992. Burrowing of the fiddler crab *Uca tangeri* in the Ria Formosa in Portugal and its influence on sediment structure. Marine Ecology Progress Series 85, 237–243.
- Yamamuro, M., Koike, I., 1994. Diel changes of nitrogen species in surface and overlying water of an estuarine lake in summer: evidence for benthic-pelagic coupling. Limnology and Oceanography 39, 1726–1733.