La mer 45 : 117-134, 2007
Société franco-japonaise d'océanographie, Tokyo

Role of tidal flat in material cycling in the coastal sea

Yumiko YARA[1]*, Tetsuo YANAGI[2], Shigeru MONTANI[3] and Kuninao TADA[4]

Abstract: A simple tidal flat model with pelagic and benthic ecosystems was developed in order to analyze the nitrogen cycling in an inter–tidal flat of the Seto Inland Sea, Japan. After the verification of calculation results with the observed results in water quality and benthic biomasses, the role of this tidal flat in nitrogen cycling was evaluated from the viewpoint of water quality purification capability. When there is no suspension feeder in the tidal flat, the water quality purification capability of this tidal flat becomes lower because the outflow of organic nitrogen increases compared to the present case, and the red tides may be generated.

Keywords: *tidal flat, ecosystem model, nitrogen cycling, water quality purification capability*

1. Introduction

A tidal flat is known as the important place for the biological production in the coastal sea. Moreover a tidal flat is paid to attention because the removing function of bio–elements such as nitrogen and phosphorus from the water column is very high. NAKATA and HATA (1994) claims that the material cycling (mineralization or organization of bio–elements) in the tidal flat determines the water purification function there. SASAKI (2001) qualitatively points out that bivalves in the tidal flat play an important role in the water purifying function in the coastal sea. It is necessary to clarify the material cycling and budget quantitatively in order to understand the ecosystem characteristics and the purification function of the tidal flat. A numerical ecosystem model is a very useful tool to clarify them.

For the ecosystem model of the tidal flat, the Ems–Dollard ecosystem model (BARETTA and RUARDIJ, 1988) is very famous. Their model is constructed with pelagic, benthic and epi–benthic sub–models and simulates the seasonal variation in the tidal flat ecosystem, focusing on the carbon cycling. In Japan, HATA *et al.* (1995) produced a tidal flat ecosystem model based on the Ems–Dollard ecosystem model. Their model emphasizes the benthic ecosystem, focusing on the nitrogen cycling. SOHMA *et al.* (2000) produced a new numerical ecosystem model for the tidal flat and simulated the eco–dynamics over a short–time scale (< 24h). However, these models are too complex to interpret well the calculated results.

In this paper, a simple tidal flat ecosystem model with pelagic and benthic ecosystems is developed on the basis of a pelagic ecosystem model of KAWAMIYA *et al.* (1995). We reproduce the seasonal variation of the observed nitrogen values in a tidal flat of the Seto Inland Sea, Japan from January to December 2000 using the developed simple ecosystem model. From this model results, we clarify the nitrogen cycling and budget in the tidal flat. The relation between a decrease of the biomass of

1. Department of Earth System Science and Technology, Interdisciplinary Graduate School of Engineering Science, Kyushu University, 6–1 Kasuga Koen, Kasuga, Fukuoka 816–8580, Japan
*Present address:
Graduate School of Environmental Science Hokkaido University, Kita 10 Nishi 5, Kita-ku, Sapporo 060-0813 Hokkaido, Japan
2. Research Institute for Applied Mechanics, Kyushu University, 6–1 Kasuga Koen, Kasuga, Fukuoka 816–8580, Japan
3. Graduate School of Environmental Science, Hokkaido University, Kita 13 Nishi 8, Kita–ku, Sapporo 060–0813 Hokkaido, Japan
4. Department of Life Sciences, Kagawa University, 2393 Ikenobe, Miki–cho, Kita–gun, Kagawa 761–0795, Japan

bivalve and the red tide occurrence is investigated by using this model. Finally, the role of this tidal flat is evaluated from the viewpoint of water purifying function in the coastal environment.

2. Study area and Observed data

Our study area is a sandy tidal flat located in the central part of the Seto Inland Sea, southwestern Japan (Fig. 1). The tidal flat covers an area of about 148,000 m^2 and has an average depth of 1 m with the average tidal range of about 2 m. Station B4 is an observation point of benthic biomass in the tidal flat. Stations U and K are the observation points of water characteristics above the tidal flat. Stations KA9 and KA10 are the observation points outside the tidal flat. Station M is an observation point of meteorological parameters by the Takamatsu Meteorological Observatory. There are river discharges into this tidal flat from the Shin, Kasuga and Tsumeta Rivers (Fig. 1).

Samplings were conducted every month at low tide from January to December 2000. At Stn. B4, water temperature, Dissolved Inorganic Nitrogen (DIN) and Chlorophyll. *a* (Chl. *a*) concentrations at the surface (0.0–0.5 cm) and sub-surface (0.5–2.0 cm) layers in the pore water of tidal flat were observed. Nitrogen concentration of microphytobenthos was estimated using C:Chl. *a* ratio (C:Chl. *a*=33.7:1; MONTANI *et al.*, 2003) and C:N ratio (C:N=75.7:10.1; MONTANI *et al.*, 2003). The sampling of macrozoobenthos (polychaeta and bivalve) was carried out between 0 and 10 cm depth by a 10 × 10 cm quadrat method at the same time. Nitrogen concentrations of macrozoobenthos were estimated using a linear empirical equation based on the field observations, that is, the nitrogen concentration of polychaeta N_P (gN) $=0.45 \times 0.17 \times (0.2 \times \text{total wet weight (g)})$, and that of bivalave N_B (mgN) $=96.5 \times (0.184 \times (0.167 \times \text{total wet weight (g)} +0.025) + 0.0005)$. We assume that the data at Stn. B4 are representative throughout this tidal flat shown in Fig. 1, that is, the observed data of surface and sub-surface layers in the pore water are assumed to be the data of Box 2 and Box 3 shown in Fig. 2, respectively. While, at Stns. U (water depth was 20 cm in winter and 50 cm in summer) and K (water depth was 20 cm in winter and 50 cm in summer), water temperature, salinity, DIN, Particulated Organic Nitrogen (PON) and Chl. *a* concentrations in the surface water were observed. Nitrogen concentration of phytoplankton was estimated using C:Chl. *a* ratio (C:Chl. *a*=30:1; PARSONS *et al.*, 1984) and Redfield ratio (C:N=106:16; REDFIELD *et al.*, 1963). The observations at Stns. U and K were conducted within one hour before or after the

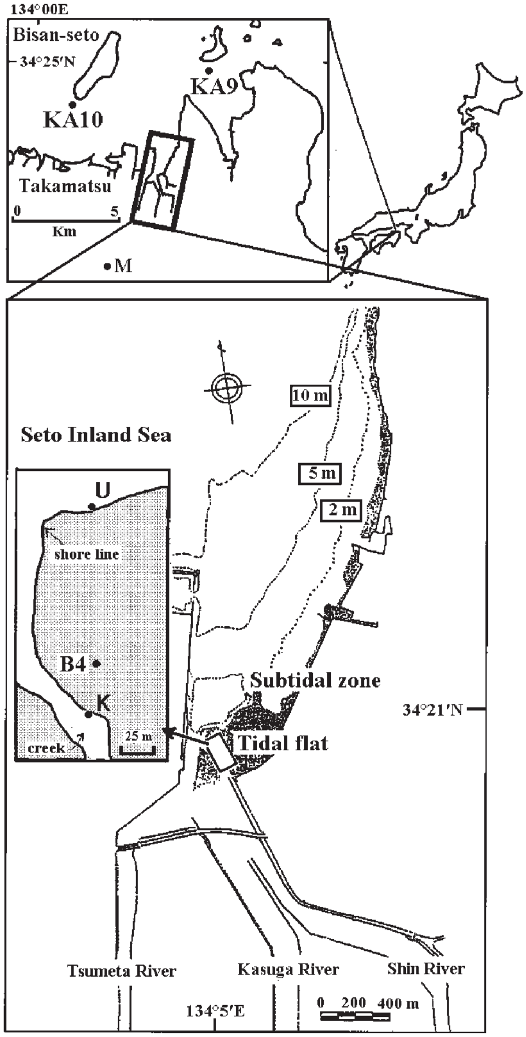

Fig. 1. Study area and location of sampling stations. Stn. B4: station for Box 2 and Box 3 in sediment, Stn. U and Stn. K: stations for Box 1 in water column, Stn. KA9 and Stn. KA10: stations for Box 4 in Bisan-seto, M: Takamatsu Meteorological Observatory.

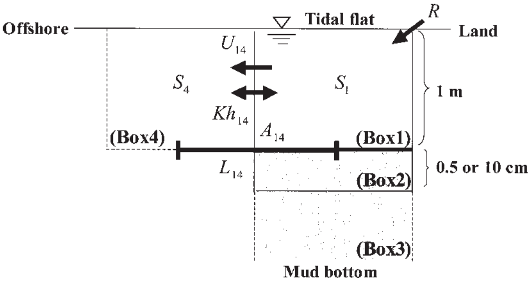

Fig. 2. Horizontal and vertical divisions of the box model. As for symbols, see the text in more detail.

observation at Stn. B4. We can expect that the water at Stn. U covers this tidal flat during the flood tidal current and that at Stn. K during the ebb tidal current, therefore the average data at Stns. U and K represent the sea–water characteristics above this tidal flat, that is, the average observed data at Stns. U and K are the data of Box 1 shown in Fig. 2.

At the same time, the observations of salinity, DIN and Chl. *a* concentrations at Stns. KA9 and KA10 in the Bisan–seto were carried out every month from January to December 2000 by the Kagawa Prefectural Fisheries Experimental Station. We assume that the average data of Stns. KA9 and KA10 are the boundary condition offshore, that is, the observed average data at Stns. KA9 and KA10 are the data of Box 4 shown in Fig. 2.

The load of Total Nitrogen (TN) from three rivers is estimated based on the monthly averaged values of river discharges from three rivers and annually averaged values of TN concentrations in three rivers. The annually averaged river discharge from three rivers and annually averaged TN concentration in three rivers in 2000 are 0.63 $m^3 s^{-1}$ and 2.4 mg L^{-1}, respectively. The monthly averaged river discharge (R) was estimated from the monthly averaged water levels in three rivers, which were measured by Kagawa Prefecture. We assumed that TN concentrations in three rivers did not change seasonally in 2000 because there was no data on the seasonal variations of TN concentrations in three rivers.

The monthly averaged data of solar radiation and wind speed in 2000 at the Takamatsu Meteorological Observatory were quoted from the Geophysical Review published by the Japan Meteorological Agency.

3. Box model

Fig. 2 shows the box model of this tidal flat. Box 1 is the pelagic ecosystem with 1 m water depth, and Box 2 is the benthic ecosystem for the benthic algae with 0 to 0.5 cm sediment depth and that for the suspension and deposit feeders with 0 to 10 cm sediment depth. We consider the pelagic ecosystem with 1 m depth above the tidal flat because the average tidal range at this tidal flat is about 2 m (MONTANI *et al.*, 2003) and we focus the annually averaged ecosystem there. The boundary condition for Box 2 is given at Box 3, and the boundary condition offshore of Box 1 is given at Box 4 in the Bisan–seto.

The horizontal advection velocity (U_{14}) and the horizontal eddy diffusivity (Kh_{14}) required for the ecosystem model calculation in this study are decided by the physical box model. The equation of water mass conservation is expressed by:

$$R = U_{14} \times A_{14} \tag{1}$$

where R ($m^3\ s^{-1}$) is the river discharge from three rivers (shown in Fig. 3 d), U_{14} ($m\ s^{-1}$) is the horizontal advection velocity between Box 1 and Box 4, A_{14} (m^2) is the cross–sectional area between Box 1 and Box 4 (shown in Table 1).

The equation of salt conservation is expressed by:

$$-U_{14} \times S_1 \times A_{14} + Kh_{14} \times \frac{S_4 - S_1}{L_{14}} \times A_{14} = 0 \tag{2}$$

where S_1 and S_4 are salinity of Box 1 and Box 4, respectively (shown in Fig. 3 c). Kh_{14} ($m^2\ s^{-1}$) is the horizontal eddy diffusivity between Box 1 and Box 4, and L_{14} (m) is the length between Box 1 and Box 4 (shown in Table 1). The temporal variation term in salinity is assumed to be zero because it is much smaller than the spatial variation terms in Eq. (2). The advection and mixing effects by tidal current is expressed by this horizontal eddy diffusivity Kh_{14} in this analysis.

U_{14} and Kh_{14} computed from equations (1) and (2) using the observed data are shown in Fig. 3 (g), (h) respectively.

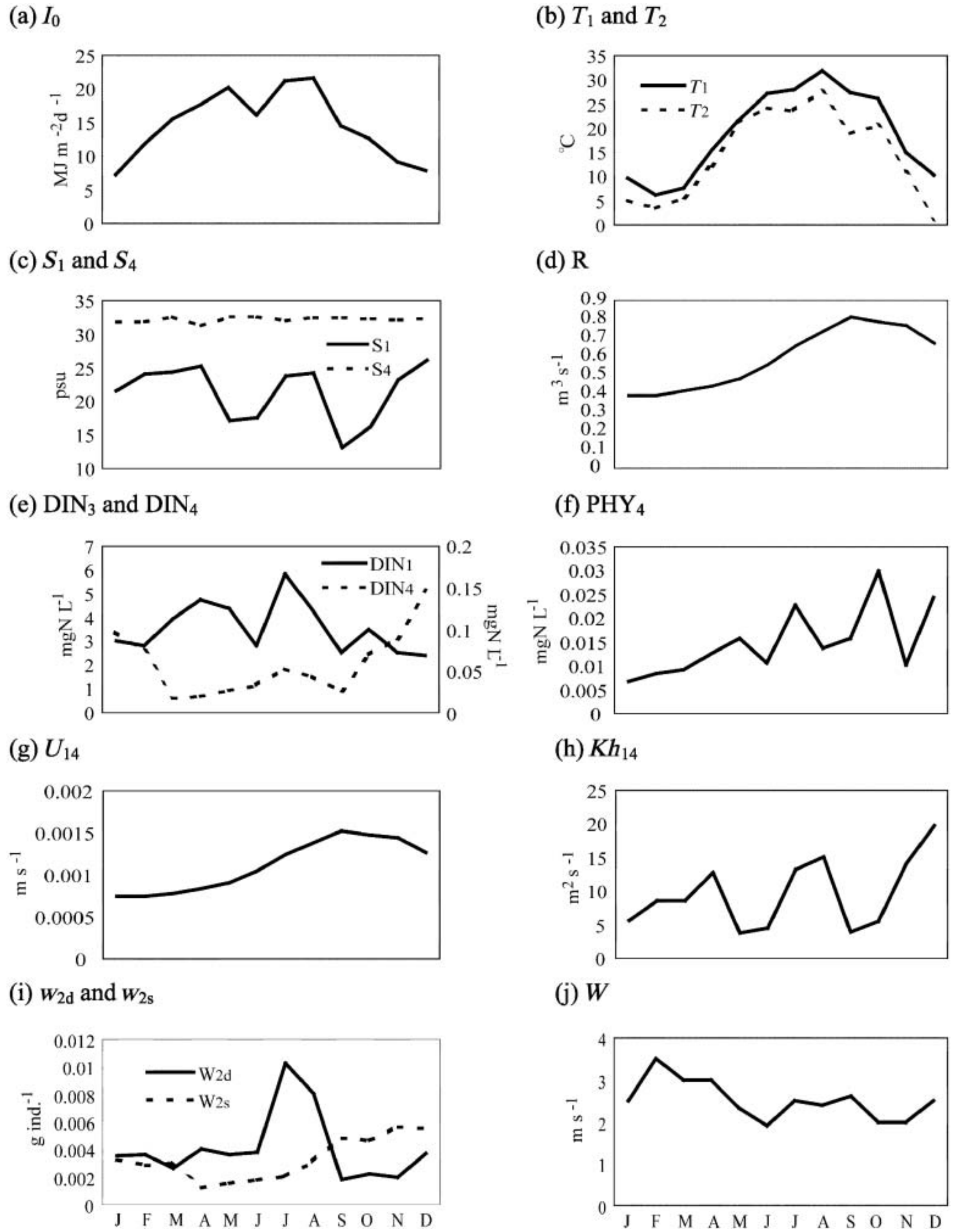

Fig. 3. Seasonal variations in monthly mean input data and boundary conditions for the model calculation. (a) I_0: solar radiation, (b) T_1: sea water temperature in Box 1 and T_2: pore water temperature in Box 2, (c) S_1 and S_4: salinity in Box 1 and Box 4, respectively, (d) R: river discharge, (e) DIN_3 (left axis) and DIN_4 (right axis) : DIN concentration in Box 3 and Box 4, respectively, (f) PHY_4: PHY concentration in Box 4, (g) U_{14}: horizontal advection velocity, (h) Kh_{14}: horizontal eddy diffusivity, (i) w_{2d}: soft-body dry weight per individual of deposit feeder and w_{2s}: soft-body dry weight per individual of suspension feeder, (j) W: monthly averaged wind speed.

Table 1 Parameters used in the model and their references.

	symbol	definition	value	unit	reference
⊿t	dt	time step	100	s	1)
physics	V_1, V_{21}, V_{22}	volume	148×10^6, 0.74×10^6, 14.8×10^6	L	–
	A_{12}・A_{23}, A_{14}	sectional area	148×10^3, 530	m^2	–
	L_{12}, L_{23}, L_{14}	distance	50.25×10^{-2}, 10^{-2}, 3750	m	–
	Kv_{12}, Kv_{23}	eddy diffusivity	7.9×10^{-6}, 6.8×10^{-8} (9.8×10^{-10})	$m^2\ s^{-1}$	tuning (2))
DET_1	W_d	sinking speed of detritus	1.0	$m\ d^{-1}$	2)
phytoplankton	Vm_1	maximum photosynthetic speed	1.0	d^{-1}	5)
	Kn_1	half saturation constant for DIN	0.16	$mgN\ L^{-1}$	4)
	k_1	temperature dependency of photosynthesis	0.063	$℃^{-1}$	5)
	$Iopt_1$	optimum light intensity for photosynthesis	50×10^5	$cal\ m^{-2}\ d^{-1}$	–
	$A2_1$	ratio of extracellular excertion of DON	0.135	–	5)
	Mpo_1	mortality rate at 0℃	8.15 (2.0)	$L\ mgN^{-1}\ d^{-1}$	tuning (5))
	Kmp_1	temperature coefficient for mortality	0.069	$℃^{-1}$	5)
zooplankton	α_G	maximum grazing speed at 0 ℃	0.4	d^{-1}	6)
	λ	Ivlev's constant	99.9	$(mgN\ L^{-1})^{-1}$	5)
	PHY^*	threshold of grazing	6.02×10^{-4}	$mgN\ L^{-1}$	5)
	k_g	temperature dependency of grazing	0.069	$℃^{-1}$	5)
	α_1	excretion generation speed	0.4	–	5)
	β_1	egestion generation speed	0.3	–	5)
	Mzo_1	mortality rate at 0℃	4.15	$L\ mgN^{-1}\ d^{-1}$	5)
	Kmz_1	temperature coefficient for mortality	0.069	$℃^{-1}$	5)
microphytobenthos	Vm_2	maximum photosynthetic speed	1.68	d^{-1}	3)
	Kn_2	half saturation constant for DIN	0.16	$mgN\ L^{-1}$	4)
	$A2_2$	ratio of extracellular excertion of DON	0.135	–	5)
	Mpo_2	mortality rate at 0℃	1.0×10^{-3}	$L\ mgN^{-1}\ d^{-1}$	tuning
	Kmp_2	temperature coefficient for mortality	0.069	$℃^{-1}$	5)
deposit feeder	α_{2d}	excretion generation speed	0.4	–	5)
	β_{2d}	egestion generation speed	0.3	–	5)
	Mzo_{2d}	mortality rate at 0℃	1.5×10^{-3}	$L\ mgN^{-1}\ d^{-1}$	tuning
	Kmz_{2d}	temperature coefficient for mortality	0.069	$℃^{-1}$	5)
suspension feeder	α_{2s}	excretion generation speed	0.4	–	5)
	β_{2s}	egestion generation speed	0.3	–	5)
	Mzo_{2s}	mortality rate at 0℃	1.43×10^{-4}	$L\ mgN^{-1}\ d^{-1}$	tuning
	Kmz_{2s}	temperature coefficient for mortality	0.069	$℃^{-1}$	5)
Box1 and Box2	$Vni_{1\ or\ 2}$	decomposition speed of detritus to DIN at 0℃	0.03	d^{-1}	5)
	$Kvni_{1\ or\ 2}$	temperature dependency of decomposition of detritus to DIN	0.069	$℃^{-1}$	5)
	$Vno_{1\ or\ 2}$	decomposition speed of detritus to DON at 0℃	0.03	d^{-1}	5)
	$Kvno_{1\ or\ 2}$	temperature dependency of decomposition of detritus to DON	0.069	$℃^{-1}$	5)
	$Vdi_{1\ or\ 2}$	decomposition speed of DON to DIN at 0℃	0.03	d^{-1}	5)
	$Kvdi_{1\ or\ 2}$	temperature dependency of decomposition of DON to DIN	0.069	$℃^{-1}$	5)

1) Onitsuka *et al.* (2002), 2) Hata *et al.* (1995), 3) Montani *et al.* (2003), 4) Nishijima *et al.* (1990), 5) Kawamiya *et al.* (1995), 6) Fujii *et al.* (2002)

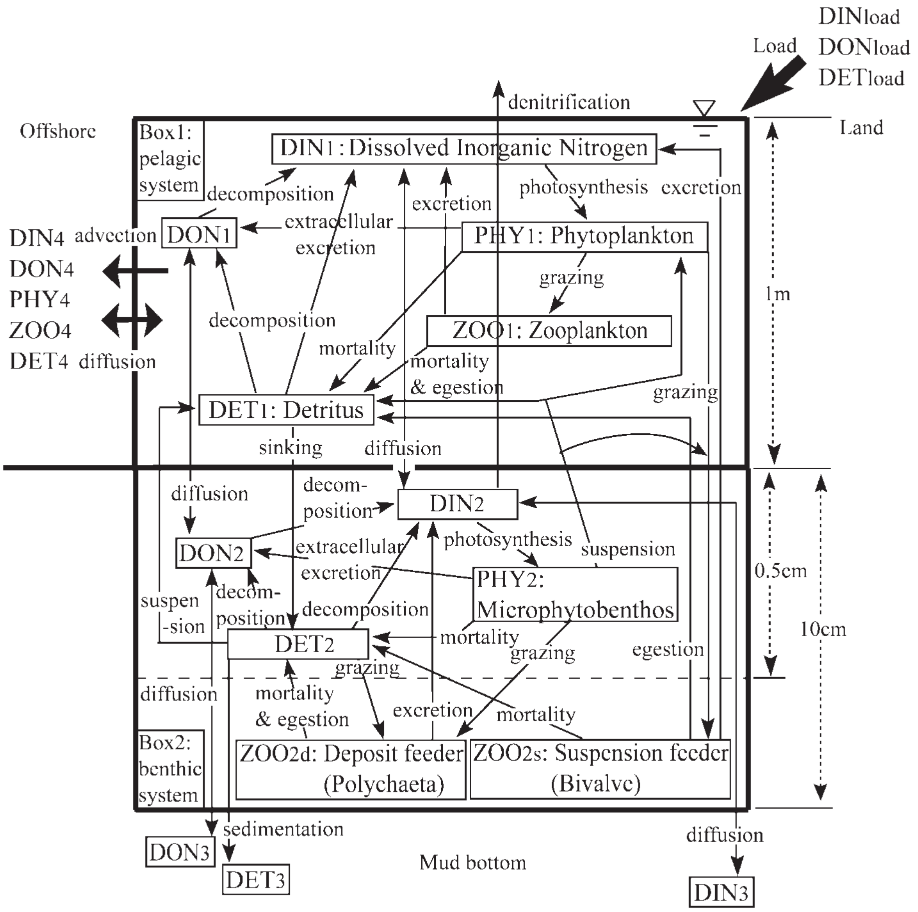

Fig. 4 Schematic diagram of nitrogen cycling in the numerical ecosystem model.

4. Ecosystem models

In the boxes of Box 1 and Box 2 (Fig. 2), a physical, biological and chemical processes concerning the nitrogen cycling shown in Fig. 4 are considered.

The compartments of Box 1 are Dissolved Inorganic Nitrogen (DIN_1), Dissolved Organic Nitrogen (DON_1), phytoplankton (PHY_1), zooplankton (ZOO_1) and detritus (DET_1) within 1 m water column. The compartments of Box 2 are Dissolved Inorganic Nitrogen (DIN_2), Dissolved Organic Nitrogen (DON_2), microphytobenthos (PHY_2) and detritus (DET_2) within 0.5 cm sediment depth, and deposit feeder "polychaeta" (ZOO_{2d}) and suspension feeder "bivalve" (ZOO_{2s}) within 10 cm sediment depth. Reproduction of seasonal variations in DIN_1, PHY_1, PON_1 (particulated organic nitrogen in Box 1$=PHY_1+ZOO_1+DET_1$), DIN_2, PHY_2, ZOO_{2d} and ZOO_{2s} concentrations at Box 1 and Box 2 is tried in this numerical experiment.

The temporal variations in 9–compartemnt concentrations at Box 1 and Box 2 are given by the following equations, based on KAWAMIYA *et al.* (1995).

$$
\begin{aligned}
V_1\frac{dDIN_1}{dt}
&=\text{Load from rivers } (DIN_{LA1})\\
&\quad-\text{Photosynthesis } (PHY_1)\\
&\quad+\text{Excretion } (ZOO_1)\\
&\quad+\text{Decomposition } (DET_1\rightarrow DIN_1)\\
&\quad+\text{Decomposition } (DET_1\rightarrow DON_1)\\
&\quad+\text{Excretion } (ZOO_{2s})\\
&\quad-\text{Vertical Diffusion } (DIN_1, DIN_2)\\
&\quad-\text{Horizontal Diffusion } (DIN_1, DIN_4)\\
&\quad-\text{Horizontal Advection } (DIN_1) \qquad (3)
\end{aligned}
$$

$$V_1\frac{d\mathrm{DON}_1}{dt}$$
= Load from rivers (DON_{LA1})
+ Extracellular excretion (PHY_1)
+ Decomposition ($DET_1 \rightarrow DON_1$)
− Decomposition ($DON_1 \rightarrow DIN_1$)
− Vertical Diffusion (DON_1, DON_2)
− Horizontal Diffusion (DON_1, DON_4)
− Horizontal Advection (DON_1) (4)

$$V_1\frac{d\mathrm{PHY}_1}{dt}$$
= Photosynthesis (PHY_1)
− Extracellular excretion (PHY_1)
− Mortality (PHY_1)
− Grazing ($PHY_1 \rightarrow ZOO_1$)
− Grazing ($PHY_1 \rightarrow ZOO_{2s}$)
− Horizontal Diffusion (PHY_1, PHY_4)
− Horizontal Advection (PHY_1)
+ Suspension (PHY_2) (5)

$$V_1\frac{d\mathrm{ZOO}_1}{dt}$$
= Grazing ($PHY_1 \rightarrow ZOO_1$)
− Excretion (ZOO_1)
− Egestion (ZOO_1)
− Mortality (ZOO_1)
− Horizontal Diffusion (ZOO_1, ZOO_4)
− Horizontal Advection (ZOO_1) (6)

$$V_1\frac{d\mathrm{DET}_1}{dt}$$
= Load from rivers (DET_{LA1})
+ Mortality (PHY_1)
+ Egestion (ZOO_1)
+ Mortality (ZOO_1)
− Decomposition ($DET_1 \rightarrow DIN_1$)
− Decomposition ($DET_1 \rightarrow DON_1$)
− Horizontal Diffusion (DET_1, DET_4)
− Horizontal Advection (DET_1)
− Sinking (DET_1)
+ Suspension (PHY_2)
+ Suspension (DET_2)
+ Egestion (ZOO_{2s}) (7)

$$V_{21}\frac{d\mathrm{DIN}_2}{dt}$$
= − Photosynthesis (PHY_2)
+ Decomposition ($DET_2 \rightarrow DIN_2$)
+ Decomposition ($DON_2 \rightarrow DIN_2$)
+ Excretion (ZOO_{2d})
− Vertical Diffusion (DIN_2, DIN_3)
− Horizontal Diffusion (DIN_2, DIN_1)
− Nitrification (DIN_2) (8)

$$V_{21}\frac{d\mathrm{DON}_2}{dt}$$
= Extracellular excretion (PHY_2)
+ Decomposition ($DET_2 \rightarrow DON_2$)
− Decomposition ($DON_2 \rightarrow DIN_2$)
− Vertical Diffusion (DON_2, DON_3)
− Vertical Diffusion (DON_2, DON_1) (9)

$$V_{21}\frac{d\mathrm{PHY}_2}{dt}$$
= Photosynthesis (PHY_2)
− Extracellular excretion (PHY_2)
− Mortality (PHY_2)
− Suspension (PHY_2)
− Grazing ($PHY_2 \rightarrow ZOO_{2d}$) (10)

$$V_{22}\frac{d\mathrm{ZOO}_{2d}}{dt}$$
= Grazing ($PHY_2 \rightarrow ZOO_{2d}$)
+ Grazing ($DET_2 \rightarrow ZOO_{2d}$)
− Excretion (ZOO_{2d})
− Egestion (ZOO_{2d})
− Mortality (ZOO_{2d}) (11)

$$V_{22}\frac{d\mathrm{ZOO}_{2s}}{dt}$$
= Grazing ($PHY_1 \rightarrow ZOO_{2s}$)
+ Grazing ($PHY_2 \rightarrow ZOO_{2s}$)
− Excretion (ZOO_{2s})
− Egestion (ZOO_{2s})
− Mortality (ZOO_{2s}) (12)

$$V_{21}\frac{d\mathrm{DET}_2}{dt}$$
= Mortality (PHY_2)
− Decomposition ($DET_2 \rightarrow DIN_2$)
− Decomposition ($DET_2 \rightarrow DON_2$)
− Suspension (DET_2)
− Grazing ($DET_2 \rightarrow ZOO_{2d}$)
+ Egestion (ZOO_{2d})
+ Mortality (ZOO_{2d})
+ Mortality (ZOO_{2d})
+ Sinking (DET_1)
− Sediment (DET_2) (13)

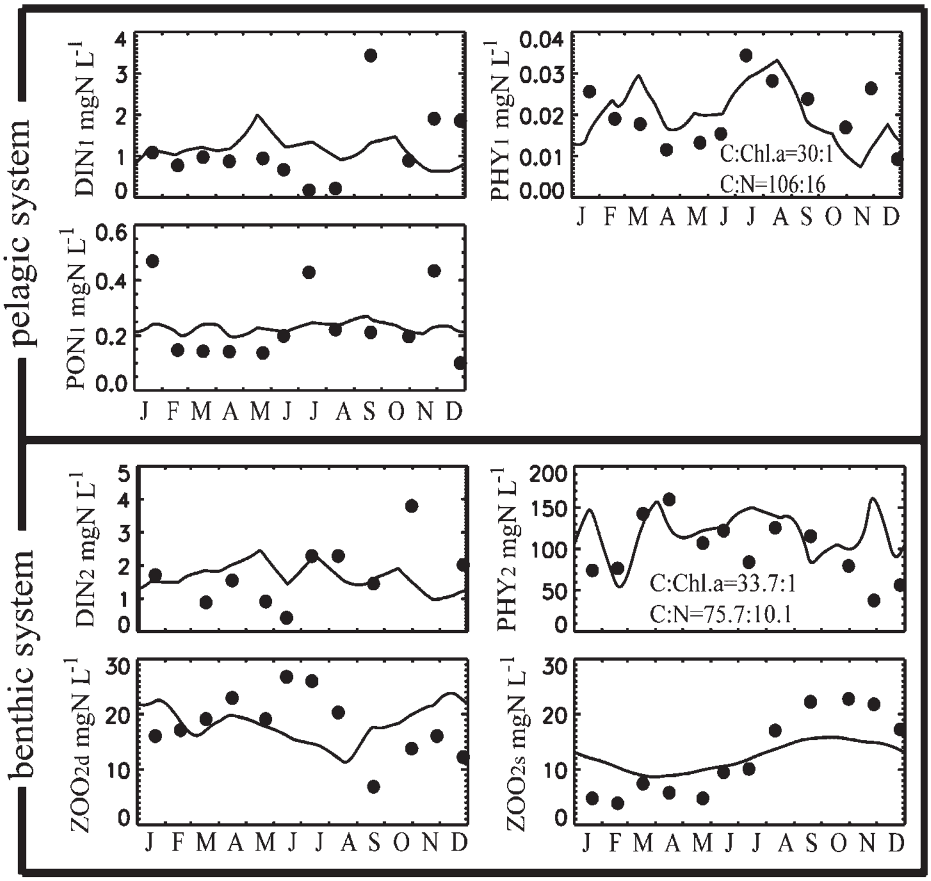

Fig. 5. Seasonal variations in calculated (full line) and observed (dot) values of DIN_1, PHY_1, PON_1, DIN_2, PHY_2, ZOO_{2d}, and ZOO_{2s} in the tidal flat of the Seto Inland Sea.

The details of each term are described in Appendix.

Parameters used in this numerical experiment are shown in Table 1. Almost all parameters are the values referred from the references. The major differences between our parameters and those of references are 1) the vertical eddy diffusivity between Box 2 and Box 3 ($Kv_{23}=6.8\times10^{-8}$ m^2 s^{-1}), that is, vertical eddy diffusivity for the pore water in our model is larger than that of HATA *et al.* (1995) (9.8×10^{-10} m^2 s^{-1}), 2) the sinking speed of detritus and mortality of phytoplankton at 0 ℃ are larger than those from the references. Tuning 1) is necessary for reproducing DIN_2 concentration and 2) for reproducing PON_1 and PHY_1 concentrations. While the mortalities of microphytobenthos (PHY_2), deposit feeder (ZOO_{2d}) and suspension feeder (ZOO_{2s}) are tuned to reproduce their observed concentrations because there is no reference on these parameters.

Figure 3 shows the input data and boundary conditions for the model calculation. We assume that Dissolved Organic Nitrogen in Box 3 (DON_3), that in Box 4 (DON_4), zooplankton in Box 4 (ZOO_4) and detritus in Box 4 (DET_4) concentrations are equal to DIN in Box 3 (DIN_3), that in Box 4 (DIN_4), 0.1 times phytoplankton in Box 4 (PHY_4) and DIN_4, respectively. The loads of DIN, DON and DET from rivers are given as 45, 22 and 33 % of TN load from three rivers, respectively, based on the results of field observation (Dr. K. ICHIMI, personal communication).

The initial conditions for model compartments are given by setting the annually

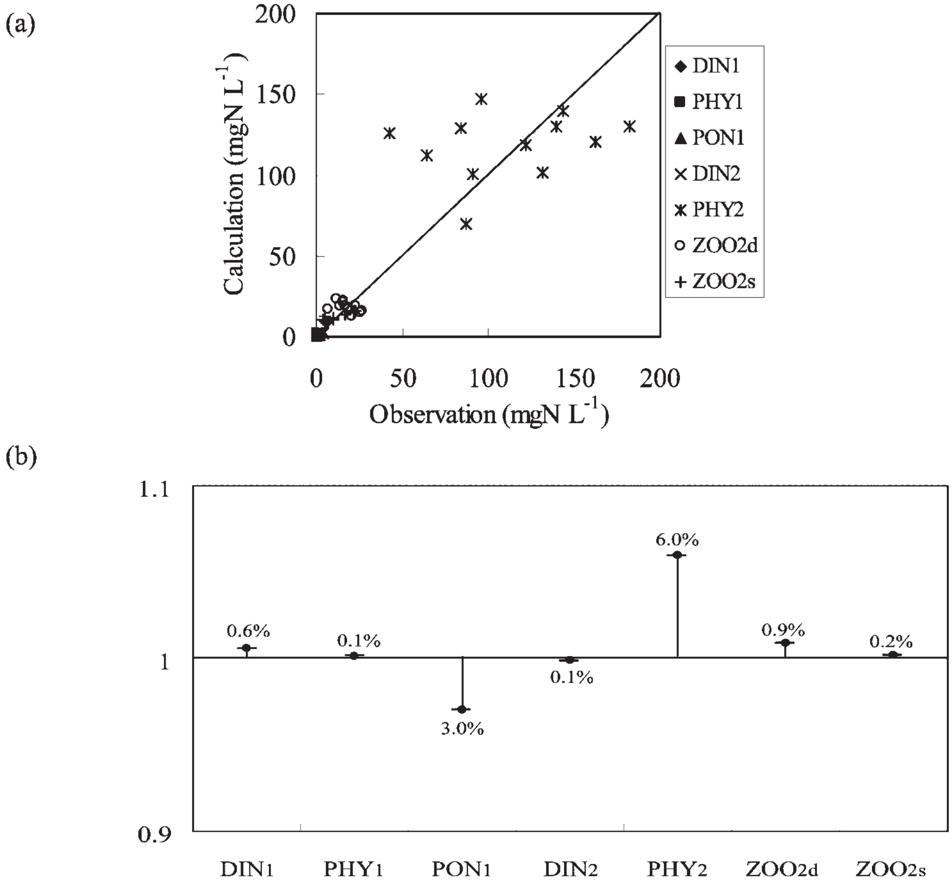

Fig. 6. (a) Correlation between observed and calculated values of nitrogen concentration. (b) Ratio of the annually averaged calculated value and the annually averaged observed value.

averaged values of observed data in the tidal flat. The integration was carried out with a time step of 100 seconds and quasi–steady seasonal variations were obtained 3 years after the start of the calculation. The seasonal variations in the fourth year were analyzed.

5. Results and Discussion

Verification of calculation

Figure 5 shows the seasonal variations in calculated (full line) and observed (dot) DIN_1, PHY_1, PON_1, DIN_2, PHY_2, ZOO_{2d} and ZOO_{2s} concentrations at the tidal flat. The observed DIN_2 concentrations in February and November were missing. The details of seasonal variations are not reproduced enough, but the annually averaged values and phases of seasonal variations are roughly reproduced by our model. Therefore we may consider that this model results reproduce the annually averaged situation of this tidal flat.

Figure 6 (a) shows a correlation between observed and calculated values of nitrogen concentration. Only PHY_2 values are very high because they are concentrated at the surface of bottom mud of tidal flat. The correlation coefficient and the root mean squared error are 0.93 and 15.9 mgNL^{-1}, respectively. Fig. 6 (b) shows the ratio of the annually averaged calculated value to the annually averaged observed value of each compartment. We can understand that the differences between the calculated and observed values of each compartment are less than 6.0 % from Fig. 6 (b). After this, our discussion will be focused on the annually averaged values.

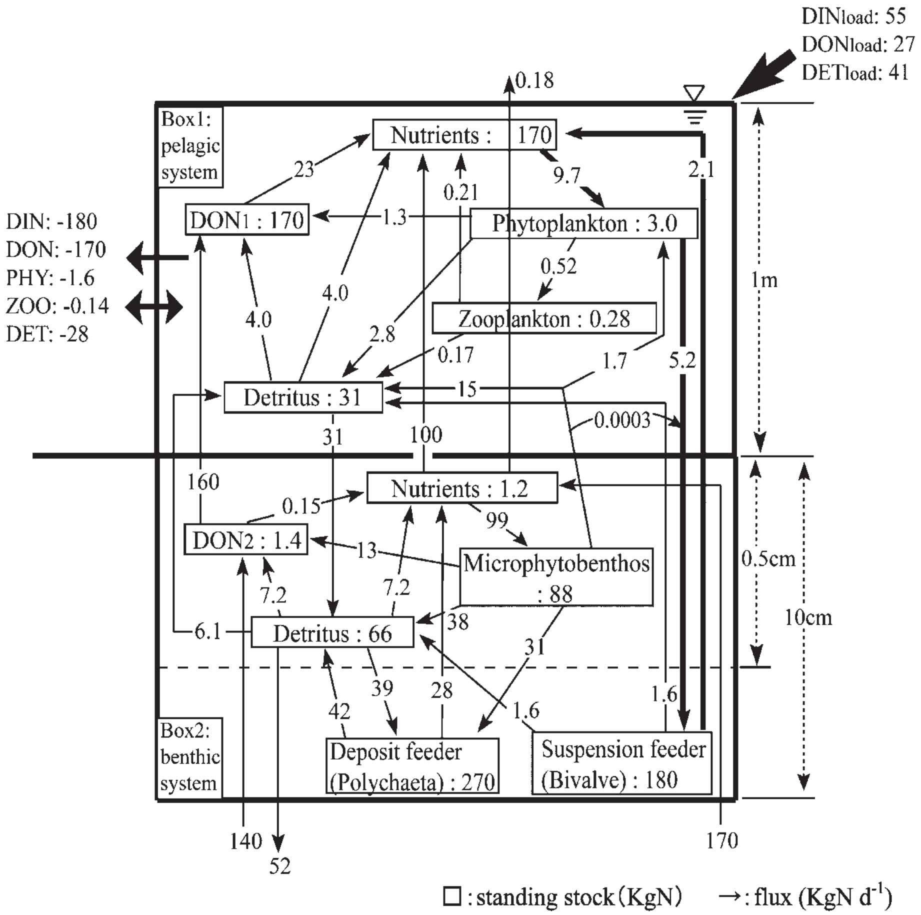

Fig. 7. Annually averaged values of nitrogen standing stocks (KgN) and their fluxes (KgN d^{-1}) in the tidal flat of the Seto Inland Sea. Thick arrows show the main pathway.

Present case and the case where there is no suspension feeder (bivalve)

Figure 7 shows the annually averaged values of nitrogen standing stocks and their fluxes in the present case with the suspension feeder (bivalve) at the tidal flat. The numbers in the small box show the standing stocks with the unit of KgN. The numbers on the arrow show the fluxes with the unit of KgN d^{-1}. The main pathway of the nitrogen cycling in the tidal flat was nutrients in Box 1 (DIN_1) →phytoplankton (PHY_1) →suspension feeder (ZOO_{2s}) → nutrients in Box 1 (DIN_1). The suspension feeder plays an important role in the exchange of nitrogen between the pelagic and benthic ecosystems in the tidal flat.

In recent years, the standing stock of suspension feeder has dramatically decreased while the number of red tide occurrence has increased in Japanese coastal seas with tidal flats though the nutrient load from the river has not increased (e.g. TSUTUMI *et al.*, 2003). We pay our attention to the role of suspension feeder, which is known to have the water quality purification capability by filtration of suspended matter, and want to predict the phytoplankton concentration in the case where there is no suspension feeder.

Figure 8 shows the seasonal variations of calculated values in the present case with the suspension feeder (solid line) and in the case where there is no suspension feeder (broken line). When there is no suspension feeder (ZOO_{2s}) in the tidal flat, the nitrogen concen-

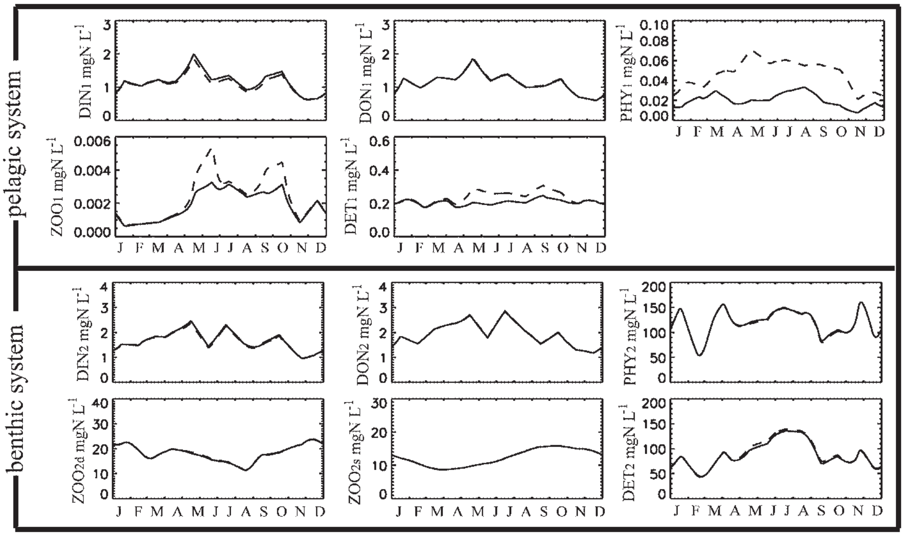

Fig. 8. Seasonal variations of calculated values in the present case with the suspension feeder (solid line) and the case where there is no suspension feeder (broken line) .

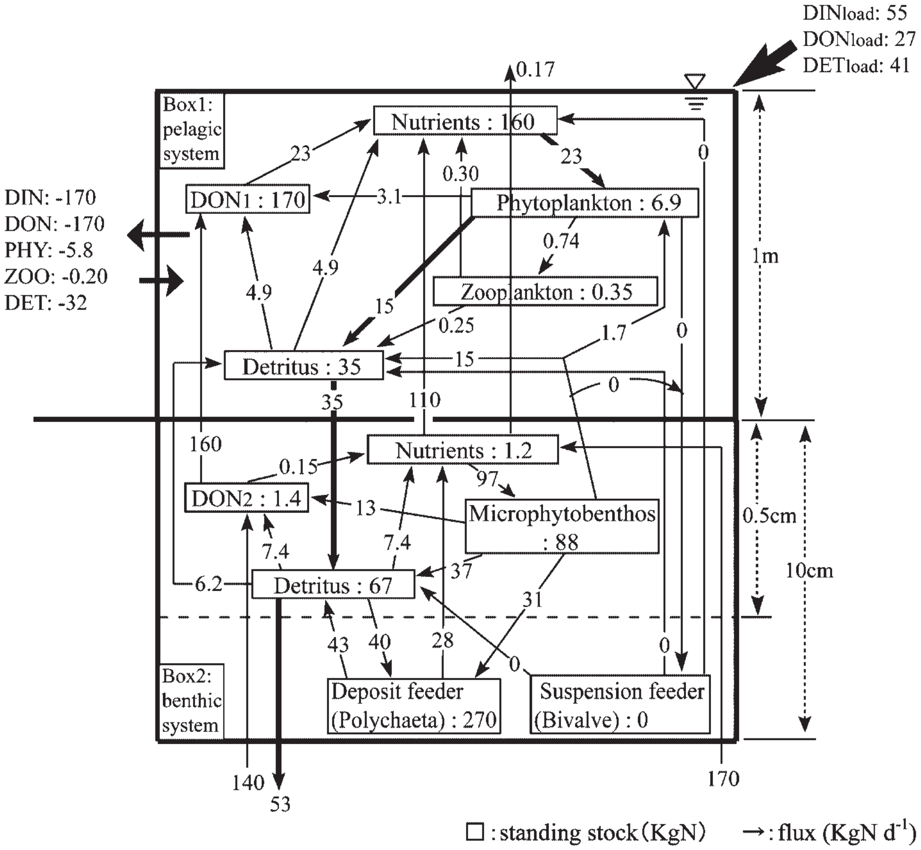

Fig. 9. Annually averaged values of nitrogen standing stocks (KgN) and their fluxes (KgN d^{-1}) in the case where there is no suspension feeder at the tidal flat. Thick arrows show the main pathway.

trations of phytoplankton (PHY_1), zooplankton (ZOO_1) and detritus (DET_1) in Box 1, and detritus (DET_2) in Box 2 increase and the nitrogen concentration of nutrient in Box 1 (DIN_1) decreases.

The nitrogen concentration of phytoplankton (PHY_1) in Box 1 is about 2.3 times as high as the present case because of the vanishing of

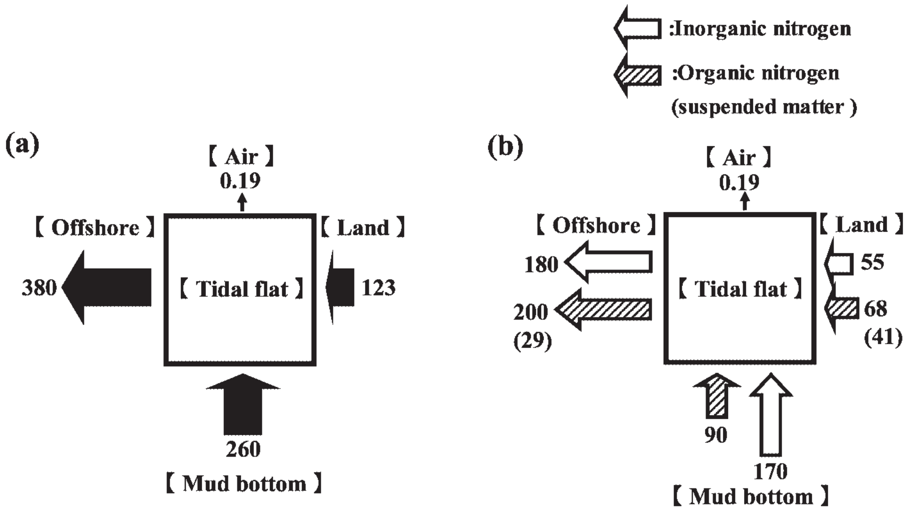

Fig. 10. Annually averaged values of nitrogen budget (a) and inorganic and organic nitrogen budgets (b) in the present case with the suspension feeder.

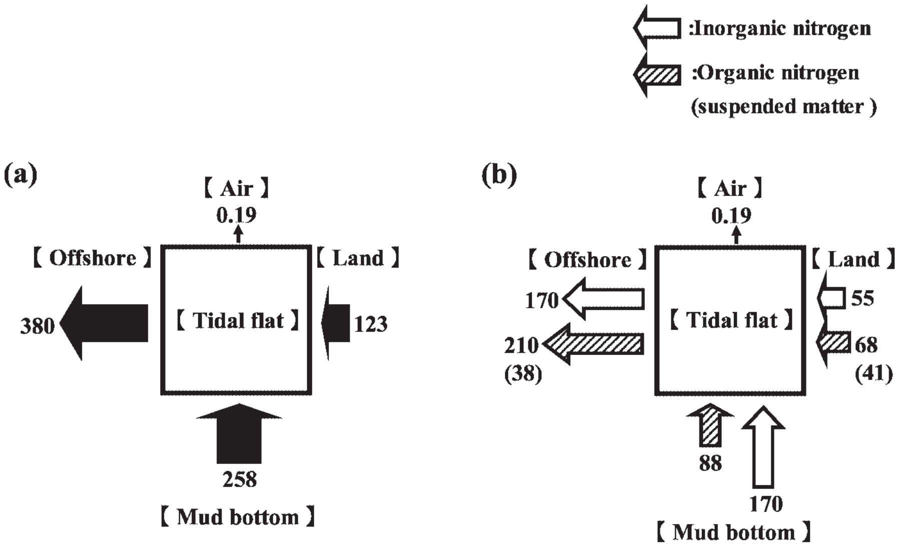

Fig. 11. Annually averaged values of nitrogen budget (a) and inorganic and organic nitrogen budgets (b) in the case where there is no suspension feeder (bivalve) .

grazing pressure and the red tide (PHY_1 concentration of 0.053 mgN L^{-1} corresponds to 10 μgChl. a L^{-1} which is the red tide concentration of diatom) may occur.

Figure 9 shows the annually averaged values of nitrogen standing stocks and their fluxes in the case where there is no suspension feeder at the tidal flat. The main pathway of the nitrogen cycling becomes nutrients in Box 1 (DIN_1) →phytoplankton (PHY_1) →detritus in Box 1 (DET_1) →detritus in Box 2 (DET_2).

Water quality purification capability

There are various viewpoints about the purification capability in the coastal sea (e.g. NAKATA and HATA, 1994; HATA *et al.*, 1995; 1996; 2004; SUZUKI *et al.*, 1997). In this paper, we define the purification capability as follows. One is the conversion from organic nitrogen to inorganic nitrogen (that is, mineralization). The other is the reduction of suspended matter being transported offshore (that is, removal capability of the suspended matter from the water column). In order to evaluate the purification capability of the tidal flat, we pay attention to the nitrogen budget in this tidal flat (Fig. 10 (a) and Fig. 11 (a)), and divide their budgets into inorganic nitrogen and organic nitrogen in this tidal flat (Fig. 10 (b) and Fig. 11 (b)). Figures 10 and 11 are made from Fig. 7 and Fig. 9, and they show the annually averaged values of nitrogen budget (a) and inorganic and organic nitrogen budgets (b) in the present case with the suspension feeder (Fig. 10) and the case where there is no suspension feeder (Fig. 11) at the tidal flat, respectively.

From the comparison of Fig. 10 (a) with Fig. 11 (a), we can understand that, in the case where there is no suspension feeder (Fig. 11 (a)), the nitrogen flux from the tidal flat to the mud bottom is smaller than that in the present case because the increase of detritus deposition. The detritus which is deposited to the mud bottom causes the degradation of the marine environment in this tidal flat.

To evaluate the water quality purification capability, we pay attention to the nitrogen fluxes from the land to the tidal flat (inflow) and from the tidal flat to the offshore (outflow) in Figs.10 and 11.

From the comparison of Fig. 10 (b) and Fig. 11 (b), the water quality purification capability of the tidal flat in the case where there is no suspension feeder is lower because the outflow of organic nitrogen increases and that of inorganic nitrogen decreases compared to those in the present case.

6. Conclusion

A simple tidal flat model with pelagic and benthic ecosystems was developed in order to analyze the nitrogen cycling in an inter–tidal flat of the Seto Inland Sea, Japan. The main pathway of the nitrogen cycling in the present tidal flat with the suspension feeder is nutrients in the pelagic system →phytoplankton → suspension feeder (bivalve) →nutrients in the pelagic system. When there is no suspension feeder in the tidal flat, the main pathway of the nitrogen cycling in the tidal flat changes into nutrients in the pelagic system →phytoplankt on →detritus in the pelagic system →detritus in the benthic system, and the concentration of phytoplankton is about 2.3 times as high as that in the present case with the suspension feeder. It results in the occurrence of red tide in the tidal flat. From the view point of the water quality purification capability of tidal flat, the water quality purification capability of the tidal flat becomes lower in the case without the suspension feeder in the tidal flat because the outflow of organic nitrogen increases compared to that in the present case.

The material cycling in the tidal flat is greatly changed by the change of benthic communities there and at the same time, the water purification capability of the tidal flat will be changed. The suspension feeder plays a very important role in the water purification capability of tidal flat.

Appendix

The seasonal variations in 9–component concentrations (mgN L^{-1} except g L^{-1} of ZOO_{2d}^* and ZOO_{2s}^* which are a soft–body dry weight) at Box 1 and Box 2 are given by the following equations. Governing equations and ecosystem processes are based on KAWAMIYA *et al.* (1995).

$$V_1 \frac{d\mathrm{DIN}_1}{dt}$$

=Load from rivers ($\mathrm{DIN}_{\mathrm{LA1}}$)
−Photosynthesis (PHY_1)
+Excretion (ZOO_1)
+Decomposition ($\mathrm{DET}_1 \rightarrow \mathrm{DIN}_1$)
+Decomposition ($\mathrm{DET}_1 \rightarrow \mathrm{DON}_1$)
+Excretion (ZOO_{2s})
−Vertical Diffusion (DIN_1 , DIN_2)
−Horizontal Diffusion (DIN_1, DIN_4)
−Horizontal Advection (DIN_1)

$$= DIN_{\mathrm{LA1}} + V_1 (-A1_1\, \mathrm{PHY}_1 + B2_1\, \mathrm{ZOO}_1 + C1_1\, \mathrm{DET}_1 + D1_1\, \mathrm{DON}_1) + V_{22}\, B2_{2s}\, \mathrm{ZOO}_{2s} - A_{12} \frac{Kv_{12}}{L_{12}} (\mathrm{DIN}_1 - \mathrm{DIN}_2) - A_{14} \frac{Kh_{14}}{L_{14}} (\mathrm{DIN}_1 - DIN_4) - A_{14}\, U_{14}\, \mathrm{DIN}_1 \qquad \text{(A1)}$$

$$V_1 \frac{d\mathrm{DON}_1}{dt}$$

=Load from rivers ($\mathrm{DON}_{\mathrm{LA1}}$)
+Extracellular excretion (PHY_1)
+Decomposition ($\mathrm{DET}_1 \rightarrow \mathrm{DON}_1$)
−Decomposition ($\mathrm{DON}_1 \rightarrow \mathrm{DIN}_1$)
−Vertical Diffusion (DON_1, DON_2)
−Horizontal Diffusion (DON_1, DON_4)
−Horizontal Advection (DON_1)

$$= DON_{\mathrm{LA1}} + V_1 (A1_1\, A2_1\, \mathrm{PHY}_1 + C2_1\, \mathrm{DET}_1 - D1_1\, \mathrm{DON}_1) - A_{12} \frac{Kv_{12}}{L_{12}} (\mathrm{DON}_1 - \mathrm{DON}_2) - A_{14} \frac{Kh_{14}}{L_{14}} (\mathrm{DON}_1 - DON_4) - A_{14} U_{14}\, \mathrm{DON}_1 \qquad \text{(A2)}$$

$$V_1 \frac{d\mathrm{PHY}_1}{dt}$$

=Photosynthesis (PHY_1)
−Extracellular excretion (PHY_1)
−Mortality (PHY_1)
−Grazing ($\mathrm{PHY}_1 \rightarrow \mathrm{ZOO}_1$)
−Grazing ($\mathrm{PHY}_1 \rightarrow \mathrm{ZOO}_{2s}$)
−Horizontal Diffusion (PHY_1, PHY_4)
−Horizontal Advection (PHY_1)
+Suspension (PHY_2)

$$= V_1 (A1_1\, \mathrm{PHY}_1 - A1_1\, A2_1\, \mathrm{PHY}_1 - A3_1\, \mathrm{PHY}_1^2 - B1_1\, \mathrm{ZOO}_1) - V_{22}\, B1_{2s-1}\, \mathrm{ZOO}_{2s} - A_{14} \frac{Kh_{14}}{L_{14}} (\mathrm{PHY}_1 - PHY_4) - A_{14}\, U_{14}\, \mathrm{PHY}_1 + b \times c \times V_{21}\, A4_2\, \mathrm{PHY}_2 \qquad \text{(A3)}$$

$$V_1 \frac{d\mathrm{ZOO}_1}{dt}$$

=Grazing ($\mathrm{PHY}_1 \rightarrow \mathrm{ZOO}_1$)
−Excretion (ZOO_1)
−Egestion (ZOO_1)
−Mortality (ZOO_1)
−Horizontal Diffusion (ZOO_1 , ZOO_4)
−Horizontal Advection (ZOO_1)

$$= V_1 (B1_1\, \mathrm{ZOO}_1 - B2_1\, \mathrm{ZOO}_1 - B3_1\, \mathrm{ZOO}_1 - B4_1\, \mathrm{ZOO}_1^2) - A_{14} \frac{Kh_{14}}{L_{14}} (\mathrm{ZOO}_1 - ZOO_4) - A_{14}\, U_{14}\, \mathrm{ZOO}_1 \qquad \text{(A4)}$$

$$V_1 \frac{d\mathrm{DET}_1}{dt}$$

=Load from rivers ($\mathrm{DET}_{\mathrm{LA1}}$)
+Mortality (PHY_1)
+Egestion (ZOO_1)
+Mortality (ZOO_1)
−Decomposition ($\mathrm{DET}_1 \rightarrow \mathrm{DIN}_1$)
−Decomposition ($\mathrm{DET}_1 \rightarrow \mathrm{DON}_1$)
−Horizontal Diffusion (DET_1, DET_4)
−Horizontal Advection (DET_1)
−Sinking (DET_1)
+Suspension (PHY_2)
+Suspension (DET_2)
+Egestion (ZOO_{2s})

$$= DET_{\mathrm{LA1}} + V_1 (A3_1\, \mathrm{PHY}_1^2 + B3_1\, \mathrm{ZOO}_1 + B4_1\, \mathrm{ZOO}_1^2 - C1_1\, \mathrm{DET}_1 - C2_1\, \mathrm{DET}_1) - A_{14} \frac{Kh_{14}}{L_{14}} (\mathrm{DET}_1 - DET_4) - A_{14}\, U_{14}\, \mathrm{DET}_1 - A_{12}\, w_{\mathrm{d}}\, \mathrm{DET}_1 + (1-b) \times c \times V_{21}\, A4_2\, \mathrm{PHY}_2 + V_{21}\, A4_2\, \mathrm{DET}_2 + V_{22}\, B3_{2s}\, \mathrm{ZOO}_{2s} \qquad \text{(A5)}$$

$$V_{21} \frac{d\mathrm{DIN}_2}{dt}$$

=Photosynthesis (PHY_2)
+Decomposition ($\mathrm{DET}_2 \rightarrow \mathrm{DIN}_2$)
+Decomposition ($\mathrm{DON}_2 \rightarrow \mathrm{DIN}_2$)

$$+\text{Excretion}\ (\text{ZOO}_{2d})$$
$$-\text{Vertical Diffusion}\ (\text{DIN}_2,\ \text{DIN}_3)$$
$$-\text{Horizontal Diffusion}\ (\text{DIN}_2, \text{DIN}_1)$$
$$-\text{Nitrification}\ (\text{DIN}_2)$$
$$= V_{21}\ (-A1_2\ \text{PHY}_2 + C1_2\ \text{DET}_2 + D1_2\ \text{DON}_2)$$
$$+ V_{22}\ (B2_{2d}\quad \text{ZOO}_{2d}\ )$$
$$-A_{23}\frac{Kv_{23}}{L_{23}}\ (\text{DIN}_2 - DIN_3)$$
$$-A_{12}\frac{Kv_{12}}{L_{12}}\ (\text{DIN}_2 - \text{DIN}_1)$$
$$-A_{12}\ E1_2\ \text{DIN}_2 \tag{A6}$$

$$V_{21}\frac{d\text{DON}_2}{dt}$$
$$=\text{Extracellular excretion}\ (\text{PHY}_2)$$
$$+\text{Decomposition}\ (\text{DET}_2 \rightarrow \text{DON}_2)$$
$$-\text{Decomposition}\ (\text{DON}_2 \rightarrow \text{DIN}_2)$$
$$-\text{Vertical Diffusion}\ (\text{DON}_2,\ \text{DON}_3)$$
$$-\text{Vertical Diffusion}\ (\text{DON}_2,\ \text{DON}_1)$$
$$= V_{21}\ (A1_2\ A2_2\ \text{PHY}_2 + C2_2\ \text{DET}_2 - D1_2\ \text{DON}_2)$$
$$-A_{23}\frac{Kv_{23}}{L_{23}}\ (\text{DON}_2 - DON_3)$$
$$-A_{12}\frac{Kv_{12}}{L_{12}}\ (\text{DON}_2 - \text{DON}_1) \tag{A7}$$

$$V_{21}\frac{d\text{PHY}_2}{dt}$$
$$=\text{Photosynthesis}\ (\text{PHY}_2)$$
$$-\text{Extracellular excretion}\ (\text{PHY}_2)$$
$$-\text{Mortality}\ (\text{PHY}_2)$$
$$-\text{Suspension}\ (\text{PHY}_2)$$
$$-\text{Grazing}\ (\text{PHY}_2 \rightarrow \text{ZOO}_{2d})$$
$$= V_{21}\ (A1_2\ \text{PHY}_2 - A1_2\ A2_2\ \text{PHY}_2 - A3_2\ \text{PHY}_2^2$$
$$-A4_2\ \text{PHY}_2)$$
$$-V_{22}\ (B1_{2d-1}\ \text{ZOO}_{2d}) \tag{A8}$$

$$V_{22}\frac{d\text{ZOO}_{2d}}{dt}$$
$$=\text{Grazing}\ (\text{PHY}_2 \rightarrow \text{ZOO}_{2d})$$
$$+\text{Grazing}\ (\text{DET}_2 \rightarrow \text{ZOO}_{2d})$$
$$-\text{Excretion}\ (\text{ZOO}_{2d})$$
$$-\text{Egestion}\ (\text{ZOO}_{2d})$$
$$-\text{Mortality}\ (\text{ZOO}_{2d})$$
$$= V_{22}\ (B1_{2d-1}\ \text{ZOO}_{2d}{}^* + B1_{2d-2}\ \text{ZOO}_{2d}{}^*$$
$$-B2_{2d}\ \text{ZOO}_{2d}{}^* - B3_{2d}\ \text{ZOO}_{2d}{}^* - B4_{2d}\ \text{ZOO}_{2d}{}^2) \tag{A9}$$

$$V_{22}\frac{d\text{ZOO}_{2s}}{dt}$$
$$=\text{Grazing}\ (\text{PHY}_1 \rightarrow \text{ZOO}_{2s})$$
$$+\text{Grazing}\ (\text{PHY}_2 \rightarrow \text{ZOO}_{2s})$$
$$-\text{Excretion}\ (\text{ZOO}_{2s})$$
$$-\text{Egestion}\ (\text{ZOO}_{2s})$$
$$-\text{Mortality}\ (\text{ZOO}_{2s})$$
$$= V_{22}\ (B1_{2s-1}\ \text{ZOO}_{2s}{}^* + B1_{2s-2}\ \text{ZOO}_{2s}{}^* - B2_{2s}\ \text{ZOO}_{2s}{}^*$$
$$-B3_{2s}\ \text{ZOO}_{2s}{}^* - B4_{2s}\ \text{ZOO}_{2s}{}^2) \tag{A10}$$

$$V_{21}\frac{d\text{DET}_2}{dt}$$
$$=\text{Mortality}\ (\text{PHY}_2)$$
$$-\text{Decomposition}\ (\text{DET}_2 \rightarrow \text{DIN}_2)$$
$$-\text{Decomposition}\ (\text{DET}_2 \rightarrow \text{DON}_2)$$
$$-\text{Suspension}\ (\text{DET}_2)$$
$$-\text{Grazing}\ (\text{DET}_2 \rightarrow \text{ZOO}_{2d})$$
$$+\text{Egestion}\ (\text{ZOO}_{2d})$$
$$+\text{Mortality}\ (\text{ZOO}_{2d})$$
$$+\text{Mortality}\ (\text{ZOO}_{2s})$$
$$+\text{Sinking}\ (\text{DET}_1)$$
$$-\text{Sediment}\ (\text{DET}_2)$$
$$= V_{21}\ (A3_2\ \text{PHY}_2^2 - C1_2\ \text{DET}_2$$
$$-C2_2\ \text{DET}_2 - 0.5\ A4_2\ \text{DET}_2)$$
$$+V_{22}\ (-B1_{2d-2}\ \text{ZOO}_{2d} + B3_{2d}\ \text{ZOO}_{2d}$$
$$+B4_{2d}\ \text{ZOO}_{2d}{}^2 + B4_{2s}\ \text{ZOO}_{2s}{}^2)$$
$$+A_{12}\ w_d\ \text{DET}_1$$
$$-A_{23}\ S_d\ \text{DET}_2 \tag{A11}$$

Here dt is the time step in second. V is the volume in liter, subscript 1, 21 and 22 denote 0 to 1 m water depth in Box 1, 0 to 0.5 cm sediment depth in Box 2 and 0 to 10 cm sediment depth in Box 2, respectively. A is the sectional area in m^2, L is the distance in meter, U is the current velocity in m s^{-1}, Kh is the horizontal eddy diffusivity in m^2 s^{-1}, Kv is the vertical eddy diffusivity in m^2 s^{-1}, subscript 12 denotes between Box 1 and Box 2, subscript 23 denotes between Box 2 and Box 3, subscript 14 denotes between Box 1 and Box 4. w_d is the sinking speed of detritus in m s^{-1}, s_d is the sedimentation speed of detritus in m s^{-1}. Subscript LA1 denotes the load from rivers.

$A1$ is photosynthesis by primary producer and is represented by the following equation:

$$A1_1 = Vm_1\left(\frac{\text{DIN}_1}{\text{DIN}_1 + Kn_1}\right) \times \exp\ (k_1 T_1)$$
$$\times \frac{I_1}{Iopt_1} \exp\left(1 - \frac{I_1}{Iopt_1}\right) \tag{A12}$$

$$A1_2 = Vm_2\left(\frac{\text{DIN}_2}{\text{DIN}_2 + Kn_2}\right) \times \frac{(0.081 \times T_2 + 1.48)}{3.83}$$

$$\times \frac{(7.85 - \mathrm{TANH}(\frac{0.0785 - I_2}{7.85}))}{8.84} \qquad \text{(A13)}$$

where subscripts 1 and 2 denote Box 1 (or phytoplankton in Box 1) and Box 2 (or microphytobenthos in Box 2), respectively. The function of temperature and light in the photosynthesis equation by microphytobenthos (that is, the second and third term in right–hand side of Eq. (A13)) is experimental equation of MONTANI *et al.* (2003). Vm (d^{-1}) is the maximum photosynthesis speed of primary producer, Kn (mgN L^{-1}) is a half saturation constant for DIN, k_1 (℃$^{-1}$) is the temperature dependency of photosynthesis, T (℃) is water temperature, I is the average light intensity and $Iopt_1$ (cal m^{-2} d^{-1}) is optimum light intensity for photosynthesis. I_1 (converted into cal m^{-2} d^{-1}; 1 J m^{-2} d^{-1}=1/4.1868 cal m^{-2} d^{-1}) and I_2 (converted into μE m^{-2} d^{-1}; 1 MJ m^{-2} d^{-1} =4.52 E m^{-2} d^{-1}) are the average light intensity reaching the Box 1 and Box 2, respectively. They were calculated using the following equation:

$$I_1 = I_0 \times d \qquad \text{(A14)}$$
$$I_2 = I_0 \times d \times r \qquad \text{(A15)}$$

where I_0 (MJ m^{-2} d^{-1}) is the total surface radiation observed at the Takamatsu Meteorological Observatory. d is the percentage of irradiance reduction through the water column and is calculated using the following exponential equation (MONTANI *et al.*, 2003) :

$$d = \frac{95.2}{\mathrm{H}_1} \int_0^{H_1} 10^{(-0.143 Z_1)}\, dZ_1 \qquad \text{(A16)}$$

where H_1 (m) is the water depth. r is the percentage of light reduction through the sediments and is calculated using the following exponential equation (MONTANI *et al.*, 2003) :

$$r = \frac{100}{\mathrm{H}_2} \int_0^{H_2} 10^{(-1.49 Z_2)}\, dZ_2 \qquad \text{(A17)}$$

where H_2 (mm) is the sediment depth.

$A2$ is the ratio of extracellular excertion of DON accompanying photosynthesis and is given by the constant value (Table 1). Subscripts 1 and 2 denote phytoplankton in Box 1 and microphytobenthos in Box 2, respectively.

$A3$ is the mortality of primary producer and is represented by the following equation:

$$A3_1 = Mpo_1 \exp\,(kmp_1\, T_1) \qquad \text{(A18)}$$
$$A3_2 = Mpo_2 \exp\,(kmp_2\, T_2) \qquad \text{(A19)}$$

where subscripts 1 and 2 denote Box 1 (or phytoplankton in Box 1) and Box 2 (or microphytobenthos in Box 2), respectively. Mpo (L mgN^{-1} d^{-1}) is the mortality rate of primary producer at 0℃, kmp (℃$^{-1}$) is temperature coefficient for mortality.

$A4$ is the suspension speed of microphytobenthos and detritus caused by wind waves and is represented by the following equation:

$$A4 = a \times W^2 \qquad \text{(A20)}$$

where a is coefficient, W (m s^{-1}) is the wind speed. b and c are a coefficient about suspension of microphytobenthos (PHY_2). The suspended PHY_2 is assumed as follows. All of the suspended PHY_2 becomes a target as food of suspension feeder ZOO_{2s}, however, the suspended PHY_2 not eaten by suspension feeder ZOO_{2s} becomes PHY_1 (b percent) and DET_1 (1–b percent). c is a coefficient and is represented by the following equation:

$$\mathrm{c} = 1 - \frac{0.5 \times V_{22}\, CR_{2s}\, \mathrm{ZOO}_{2s}}{V_1} \qquad \text{(A21)}$$

$B1$ is the grazing by secondary producer. $B1_1$ is the grazing PHY_1 by zooplankton and is represented by the following equation:

$$B1_1 = \alpha_G \left\{1 - \exp(\lambda(\mathrm{PHY}^* - \mathrm{PHY}_1))\right\} \exp\,(k_g T_1) \qquad \text{(A22)}$$

where subscript 1 denote Box 1 (or zooplankton in Box 1). α_G (d^{-1}) is the maximum grazing speed at 0 ℃, λ ((mgN L^{-1}) $^{-1}$) is Ivlev's constant, PHY* (mgN L^{-1}) is the threshold of grazing (that is, when the concentration of phytoplankton is lower than PHY*, the grazing by zooplankton becomes zero). k_g (℃$^{-1}$) denotes the temperature dependency of grazing. The PHY_2 and DET_2 grazing by deposit feeder are based on the grazing by suspension feeder (NAKAMURA, 2004) and are represented by the following equation, respectively:

$$B1_{2d-1}=0.5\times CR_{2d}\times \mathrm{PHY}_2 \quad (A23)$$
$$B1_{2d-2}=0.5\times CR_{2d}\times \mathrm{DET}_2 \quad (A24)$$

where subscripts 2, 2d, 2d–1 and 2d–2 denote Box 2, deposit feeder in Box 2, the PHY_2 grazing by deposit feeder in Box 2, the DET_2 grazing by deposit feeder in Box 2, respectively. CR_{2d} is the clearance rate by deposit feeder and is represented by the following equation:

$$CR_{2d}=2.41\times w_{2d}^{-0.32}\times f(T_2) \quad (A25)$$

$$f(T_2)=\frac{-0.0549\times T_2^2+2.67\times T_2-11.2}{18.9} \quad (A26)$$

where w_{2d} (g ind.$^{-1}$) is soft–body dry weight of deposit feeder, f is the function of temperature. The PHY_1 and $PHY_2{}^{\dagger}$ grazing by suspension feeder are represented by the following equation (NAKAMURA, 2004), respectively:

$$B1_{2s-1}=0.5\times CR_{2s}\times \mathrm{PHY}_1 \quad (A27)$$
$$B1_{2s-2}=0.5\times CR_{2s}\times \mathrm{PHY}_2{}^{\dagger} \quad (A28)$$

$$\mathrm{PHY}_2{}^{\dagger}=\frac{V_{21}\times A4_2\times \mathrm{PHY}_2}{V_1} \quad (A29)$$

where subscripts 2s, 2s–1 and 2s–2 denote suspension feeder in Box 2, the PHY_1 and $PHY_2{}^{\dagger}$ grazing by suspension feeder in Box 2, respectively. $\mathrm{PHY}_2{}^{\dagger}$ is the suspended PHY_2 in Box 1. CR_{2s} is the clearance rate by suspension feeder and is represented by the following equation:

$$CR_{2s}=2.41\times w_{2s}^{-0.32}\times f(T_1) \quad (A30)$$

$$f(T_1)=\frac{-0.0549\times T_1^2+2.67\times T_1-11.2}{18.9} \quad (A31)$$

where w_{2d} is soft–body dry weight of suspension feeder, f is the function of temperature.

$B2$ is the excretion generation speed of secondary producer and is represented by the following equation:

$$B2_1=\alpha_1 B1_1 \quad (A32)$$
$$B2_{2d}=\alpha_{2d}(B1_{2d-1}+B1_{2s-2}) \quad (A33)$$
$$B2_{2s}=\alpha_{2s}(B1_{2s-1}+B1_{2s-2}) \quad (A34)$$

where subscripts 1, 2d and 2s denote zooplankton in Box 1, deposit feeder in Box 2 and suspension feeder in Box 2, respectively. α is assumed to be proportional to the grazing $B1$.

$B3$ is the egestion generation speed of secondary producer and is represented by the following equation:

$$B3_1=\beta_1 B1_1 \quad (A35)$$
$$B3_{2d}=\beta_{2d}(B1_{2d-1}+B1_{2d-2}) \quad (A36)$$
$$B3_{2s}=\beta_{2s}(B1_{2s-1}+B1_{2s-2}) \quad (A37)$$

where subscripts 1, 2d and 2s denote zooplankton in Box 1, deposit feeder in Box 2 and suspension feeder in Box 2, respectively. β is assumed to be proportional to the grazing $B1$.

$B4$ is the mortality speed of secondary producer at 0℃ and is represented by the following equation:

$$B4_1=Mzo_1\exp(kmz_1 T_1) \quad (A38)$$
$$B4_{2d}=Mzo_{2d}\exp(kmz_{2d} T_2) \quad (A39)$$
$$B4_{2s}=Mzo_{2s}(8.5-\exp(kmz_{2s} T_1)) \quad (A40)$$

where subscripts 1, 2d and 2s denote zooplankton in Box 1, deposit feeder in Box 2 and suspension feeder in Box 2, respectively. Mzo (L mgN^{-1} d^{-1}) is the mortality of secondary producer at 0℃, kmz (℃$^{-1}$) is the temperature dependency of mortality of secondary producer.

$C1$ and $C2$ are decomposition of detritus to give DIN and DON, respectively. $C1$ and $C2$ are represented by the following equation:

$$C1_1=Vni_1\exp(kvni_1 T_1) \quad (A41)$$
$$C1_2=Vni_2\exp(kvni_2 T_2) \quad (A42)$$
$$C2_1=Vno_1\exp(kvno_1 T_1) \quad (A43)$$
$$C2_2=Vno_2\exp(kvno_2 T_2) \quad (A44)$$

where subscripts 1 and 2 denote Box 1 and Box 2. Vni (d^{-1}) is decomposition speed of detritus to DIN at 0℃, Vno (d^{-1}) is decomposition speed of detritus to DON at 0℃, $kvni$ (℃$^{-1}$) is temperature dependency of decomposition of detritus to DIN, $kvno$ is temperature dependency of decomposition of detritus to DON.

$D1$ is decomposition of DON to DIN and is represented by the following equation:

$$D1_1=Vdi_1\exp(kvdi_1 T_1) \quad (A45)$$
$$D1_2=Vdi_2\exp(kvdi_2 T_2) \quad (A46)$$

where subscripts 1 and 2 denote Box 1 and Box 2. Vdi (d^{-1}) is decomposition speed of DON to DIN at 0℃, $kvdi$ (℃$^{-1}$) is temperature dependency of decomposition of DON to DIN.

$E1$ is denitrification speed from Box 2 and is represented by the following equation, based on KOIKE (1991) :

$$E1 = Vde_2 \exp\ (kvde_2\ T_1) \qquad \text{(A47)}$$

where Vde_2 (d^{-1}) is denitrification speed, $kvde_2$ (℃$^{-1}$) is temperature dependency of denitrification.

References

BARETTA, J. W. and P. RUARDIJ (1988) : Tidal Flat Estuaries. Simulation and Analysis of the Ems Estuary. Ecological Studies, **71**. Springer–Verlag, Berlin, 353pp.

FUJII, M., Y. NOJIRI, Y. YAMANAKA and M. J. KISHI (2002) : A one–dimensional ecosystem model applied to time series Station KNOT. Deep–Sea Res., II, **49**, 5441–5461.

HATA, K., I. OSHIMA and K. NAKATA (1995) : Evaluation of the Nitrogen Cycle in a Tidal Flat. Estuarine and Coastal Modeling, **4**, 542–554.

HATA, K., I. OSHIMA and K. NAKATA (1996) : Evaluation of near–shore benthic nitrogen cycle using benthic ecosystem model. J. Adv. Mar. Sci. Tech. Soci, **2** (2), 31–50. (in Japanese with English abstract and captions)

HATA, K., K. NAKATA and T. SUZUKI (2004) : The nitrogen cycle in tidal flats and eelgrass beds of Ise Bay. Journal of Marine Systems, **45**, 237–253.

KAWAMIYA, M., M. KISHI, Y. YAMANAKA and N. SUGINOHARA (1995) : An ecological–physical coupled model applied to Station Papa. Journal of Oceanography, **51**, 635–664.

KOIKE, I. (1993) : Microorganisms. *In* Tokyo Bay: Its Environmental Change for Recent 100 Years. Norio Ogura (ed.), Kouseisha Kouseikaku, Tokyo, p. 102–117. (in Japanese)

MONTANI, S., P. MAGNI and N. ABE (2003) : Seasonal and interannual patterns of intertidal microphytobenthos in combination with laboratory and areal production estimates. Mar. Eco. Prog. Ser. **249**, 79–91.

NAKAMURA, K. (2004) : Suspension feeding and growth of juvenile Manila clam Ruditapes philippinarum reared in the laboratory. Fish. Sci., **70**, 215–222.

NAKATA, K. and K. HATA (1994) : Evaluation of nutrient cycle in tidal flat. J. Jpn. Soc. Water Environ, **17** (3), 158–166. (in Japanese)

NISHIJIMA, T., A. YAMATO and Y. HATA (1990) : AGP test to Skeletonema. Water Pollution Research, **13**, 173–179.

ONITSUKA, G., T. YANAGI, S. MONTANI, M. YAMADA, N. UEDA and M. SUZUKI (2002) : An Attempt to Purify Water by Culturing Mussels in Dokai Bay, Japan. Oceanography in Japan, **11** (3), 403–417. (in Japanese with English abstract and captions)

PARSONS, T. R., M. TAKAHASHI, and B. HARGRAVE (1984) : Biological Oceanographic Processes 3rd edition. Pergamon Press, 330pp.

REDFIELD, A. C., B. H. KECHUM, and F. A. RICHARDS (1963) : The influence of organisms on the composition of sea water. *In* The Sea, M. N. Hill (ed.), Interscience Pub., New York, **2**, 26–77.

SASAKI, K. (2001) : Water purification capacity of tidal flat and shallow coastal sea. Kagaku, **71**, 902–911, (in Japanese).

SOHMA, A., T. SATO and K. NAKATA (2000) : New numerical model study on a tidal flat system seasonal, daily and tidal variations. Spill Science and Technology Bulletin, **6** (2), 173–185.

SUZUKI, T., H. AOYAMA and K. HATA (1997) : The quantification of Nitrogen cycle on tidal flat by ecosystem model－In the case of Isshiki tidal flat in Mikawa bay–, J.Adv.Mar.Sci.Tech.Soci, **3** (1), 63–80. (in Japanese with English abstract and captions)

TSUTSUMI, H., E. OKAMURA, M. OGAWA, T. TAKAHASHI, K. YAMAGUCHI, S. MONTANI, N. OHASHI, T. ADACHI and T.KOMATSU (2003) : Rekations among the oxygen deficient water mass, red tide and marine structure in the head of Ariake Bay in recent years. Oceanography in Japan, **12**, 85–96 (in Japanese with English abstract and captions).

Received November 9, 2006
Accepted October 19, 2007