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ESTIMATION OF PARTICULATE ORGANIC CARBON FLUX PRODUCED FROM EELGRASS, ZOSTERA MARINA L., IN A SUBARCTIC ESTUARY OF HOKKAIDO, JAPAN

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Abstract

Akkeshi Lake is a typical subarctic estuary located in Hokkaido, Japan; it is covered with eelgrass, specifically *Zostera marina*. The oyster *Crassostrea gigas* is cultured throughout the lake, except for on the intertidal sand flats, where the Manila clam, *Ruditapes philippinarum*, is cultured near the mouth of the lake. To estimate the particulate organic carbon (POC) flux of various sources, including eelgrass, flowing out from Akkeshi Lake to Akkeshi Bay and to evaluate the role of eelgrass in carbon transport, we developed an ecosystem model that includes phytoplankton, zooplankton, dissolved inorganic matter (DIM), dissolved organic matter (DOM), particulate organic matter (POM), eelgrass, epiphytic algae, oysters and the Manila clam, and separated POM into eight classes according to its sources. Eelgrass and epiphytic algae are the most important sources of POC in Akkeshi Lake, especially in the litterfall season. The total POC inflow/outflow quantities to/from Akkeshi Lake during nine months from April to December was −4648 tons; according to its sources, −4414 tons (outflow) came from eelgrass and epiphytic algae, −551 tons (outflow) from oysters and the Manila clam,

145 tons (inflow) from phytoplankton and zooplankton, 383 tons (inflow) from outside sources (i.e., open sea) and −211 tons (outflow) from the river. The total POC production was approximately 75727 tons, 89% of which was from eelgrass and epiphytic algae; 7% was from oysters and the Manila clam; 3% was from phytoplankton and zooplankton; and 1% was from river.

1. Introduction

The eelgrass species *Zostera marina L.* is widely distributed along the coasts of the islands of Japan from Kyushu to Hokkaido (Tanaka et al. [32]) and represents one of the most important seagrasses in Japan. Eelgrass beds provide food and shelter for numerous marine organisms (Heck et al. [12]; Thayer et al. [33]). They absorb nutrients from the water column (Hemminga et al. [13]), prevent erosion, filter suspended solids and dispel wave energy (Fonseca et al. [9]). Hence, they contribute to water clarity, sediment deposition and maintenance of the shoreline (Short [29]). The highly productive eelgrass community, including epiphytic algae, plays an important role not only in the nutrient cycle but in the carbon cycle as well (Penhale and Smith [28]). To analyze the role of eelgrass in the material cycle in coastal regions, ecosystem models have been developed and represent powerful tools for this purpose.

Verhagen and Nienhuis [34] developed a numerical model for the growth, decomposition and distribution of eelgrass in relation to external forcing functions as a predictive tool for lake management in Lake Grevelingen, the Netherlands. In the model, the shoots (i.e., the parts of eelgrass plants attached to a rhizome) were divided into age classes to incorporate the effect of aging. The growth rate per unit biomass and relative growth rate were described as functions of external forcing variables, such as light, water temperature and internal control variables due to ageing of the plant material. The relative decomposition, or loss rate of eelgrass biomass, was described as a function of water temperature and water movements due to wind-induced waves and currents and was also dependent on age. These investigators simulated seasonal changes in eelgrass production, both above and below ground, and partially explained the vertical distribution of eelgrass based on their modeling results related to space, light and below ground biomass limitations.

Wetzel and Neckles [35] developed a numerical model for the photosynthesis and CO_2 uptake of eelgrass, based on theoretical non-linear functions for simulating

biologically controlled processes and empirical or statistical relationships for incorporating physical-chemical interactions and environmental forcing functions. They employed their model to simulate the photosynthesis and growth of eelgrass which is the dominant submerged aquatic macrophyte occurring in the lower Chesapeake Bay, USA. According to these researchers, the submarine light quantity (PAR) and temperature were the principal physical factors governing eelgrass photosynthesis and growth in their study area. However, typical in situ light and temperature conditions constrain photosynthesis and, therefore, plant growth to less than their physiologically possible potential.

Bach [3] coupled an eelgrass growth model with a one-dimensional general eutrophication model that described the growth of phytoplankton and zooplankton and nutrient dynamics. Important factors controlling eelgrass growth and distribution were included in the model: water transparency, water temperature, and water depth/topography of the water bed. He omitted factors such as the growth of epiphytes on eelgrass leaves and grazing birds and invertebrates. The eelgrass sub-model described seasonal and regional variations in the production and biomass of above- and below-ground portions of the plants. The phytoplankton and eelgrass sub-models were interrelated, especially with respect to water transparency, as water transparency depends on the phytoplankton (chlorophyll a) concentration. This model was developed and calibrated based on data from a shallow area around the island of Masnedø, Denmark.

A three-dimensional numerical physical-ecological coupled model including eelgrass was developed by Kishi and Uchiyama [20] for mariculture management in Shizugawa Bay, Japan. Their model was based on nitrogen flow and focused on the dissolved oxygen budget of this bay, where fish, shellfish, seagrass and seaweed are cultured. The model estimated the spatial distribution of particulate organic nitrogen (PON), dissolved oxygen (DO), dissolved organic nitrogen (DON), dissolved inorganic nitrogen (DIN) and accumulated matter from the mariculture of fish. It also took into consideration the effects of the feed and fish in each raft, and the loading of DIN from rivers, elucidating the oxygen cycle among ecological compartments.

In a subarctic estuary, an ecosystem model including eelgrass was developed by Oshima et al. [27]. They developed a three-dimensional physical-biological coupled model to evaluate the role of eelgrass in the nutrient cycle in Akkeshi Lake, Japan. Their model was expanded based on the method of Kawamiya et al. [19] by adding

eelgrass and the phosphorus flow. According to their results, nitrate was supplied to the lake through physical processes from outside the lake and was consumed biologically inside the lake, while phosphate was supplied from inside the lake and flowed out. To explain the discrepancy between nitrate and phosphate, these researchers carried out scenarios with and without eelgrass. In cases without eelgrass, nitrate and phosphate were both reduced by biological and chemical processes inside the lake. In cases with eelgrass, nitrate was reduced, but phosphate was produced inside the lake. They concluded the eelgrass was more important than phytoplankton in producing particulate organic matter (POM) in the studied lake. Oshima et al. [26] modified the model by including epiphytes, oysters and the Manila clam in the model to reveal the role of benthos and epiphytes on the material cycle in Akkeshi Lake. They simulated four cases: (1) a standard case, in which the nutrient release from the lake bottom corresponds to the accumulation of POM; (2) without the Manila clam; (3) without epiphytes; and (4) release × 0.01, in which nutrient release represents 1% of POM accumulation. Their conclusions were as follows: (1) clams play the most important role in the material cycle; (2) epiphytes are more important as shellfish food than phytoplankton; and (3) the amount of ammonium released from bottom mud is less than the accumulation of PON.

Previous studies have mainly focused on seasonal variations in the primary production and biomass of eelgrass and on the role of eelgrass in nutrient cycles. Although the ecology of eelgrass production has been studied, little is known about the relative amount of the transport of detrital material produced by eelgrass. Some of the plants produced within an eelgrass bed are retained and recycled in the sediments or exported in the form of leaves and POM. Detrital material exported to adjacent unvegetated areas serves an important ecological role by providing a source of nutrition for microbes and larger detritovores (Bach et al. [4]). Seagrass detrital export also plays an important role in the global ocean carbon cycle. Although seagrass carbon contributes only around 20% of the total amount of carbon buried by marine vascular plants, the absolute mass represents an enormous transfer of organic carbon and nutrients to the coastal ocean that can and does fuel the growth and reproduction of a wide array of consumers (Duarte et al. [8]). Despite abundant qualitative evidence for the trophic importance of detrital export from seagrass meadows, relatively few quantitative estimates of the magnitude of detrital fluxes exist. This is likely due to the difficulty in quantifying fluxes (Heck et al. [12]).

The objectives of the present study were to estimate the particulate organic carbon (POC) flux of various sources, including eelgrass, flowing out from Akkeshi

Lake to Akkeshi Bay, which is a subarctic estuary of Hokkaido, Japan (Figure 1(a)), and to evaluate the role of eelgrass in carbon transport. To achieve these objectives, we developed an ecosystem model that includes phytoplankton, zooplankton, dissolved inorganic matter (DIM), dissolved organic matter (DOM), particulate organic matter (POM), eelgrass, epiphytic algae, oysters and the Manila clam, and the model results compared with the observation data.

2. Study Area and Observations

Akkeshi Lake is located at 43°03′N 144°51′E in the eastern part of Hokkaido, which is the northern island of Japan (Figure 1(a)). The lake is semi-closed and connected to Akkeshi Bay, which is open to the North Pacific, via only a narrow channel (ca. 500m wide). The Bekanbeushi River flows into the lake. The surface area of the lake is ca. $35km^2$, and the water depth is usually less than 2m (average 1m). The shallow areas are covered with eelgrass, specifically *Zostera marina*. The major current is mainly governed by local wind, river discharge and tidal forcing (Oshima et al. [27]). From December to March, the lake is covered by ice (Iizumi et al. [15]). Oysters are cultured throughout the lake, except for on the intertidal sand flats, where the Manila clam is cultured near the mouth of the lake. The horizontal distribution of eelgrass and cultured shellfishes in the study area obtained from satellite data (Komatsu et al. [21]) and previous studies (Iizumi et al. [15]; Oshima et al. [27]; Oshima et al. [26]) is shown in Figure 1(b). Observations were carried out at 11 stations: Akkeshi Bay (stations B1~B6), Akkeshi Lake (stations L1~L4) and Bekanbeushi River (station R1) (Figure 1(a)).

Water sampling was conducted from a boat every month from April 2006 to December 2007, except during the ice-cover season (Akkeshi Bay in 2006; Akkeshi Lake in 2006 and 2007; Bekanbeushi River in 2007). Water samples were collected in two layers at each station: at the surface and 30 cm above the bottom of Akkeshi estuary. The chlorophyll a concentration was determined fluorometrically with a Turner Designs model-10. N, N-dimethylformamide (DMF) was used for the extraction of chlorophyll a. POM was filtered through a Whatman GF/F filter and dried at 60°C until constant weight. The POC and PON on the filter were determined with a CHN analyzer. Nutrient concentrations (nitrate and phosphate) were determined with a Technicon Auto Analyzer II. Zooplankton was also collected with a NORPAC plankton net (mesh size, 315μm; diameter, 45cm) in Akkeshi Lake and Bay.

The eelgrass and epiphytic algae biomasses were monitored every month at the center of Akkeshi Lake (station L2) from April to December 2006. Four samples were collected using $0.25\text{m}^2 (0.5 \times 0.5\text{m})$ quadrats. After counting the shoot number in a quadrat, eelgrass shoots were separated into aboveground and belowground portions. Plant bodies were washed and then dried at 60°C for 48 hours to measure the dry weight. After this measurement, the eelgrass was milled for measurements of the carbon and nitrogen content in the aboveground portion. Epiphytic samples were obtained from five eelgrass shoots collected separately from the quadrat sampled for determination of eelgrass biomass. Epiphytes were removed from leaf blades using a brush and collected on GF/F filters for chlorophyll a, carbon and nitrogen measurements. The chlorophyll a concentration of the epiphytes was determined using a fluorometer (Turner Designs model-10) after extraction with DMF. The carbon and nitrogen content of the eelgrass and epiphytes were measured using an element analyzer (FlashEA112, Thermo-Finnigan).

Furthermore, the inflow/outflow quantities of eelgrass litter were determined by conducting measurements of surface-drifting leaves and leaf fragments of eelgrass at the lake mouth under Akkeshi Large Bridge (station L4) on August 18th and September 20th 2008. Surface-drifting eelgrass material was collected with a 2-mm mesh net (0.7m diameter, 1m long) on a boat. A cross-section of the lake mouth was equally divided into nine sections, and a boat was used to move among the sections. Surface-drifting leaves and leaf fragments of eelgrass were collected for a minute every hour in each section from 4:00 to 16:00 (12 hours), and the wet weight was measured. The inflow and outflow quantities measured in the wet weight were converted into dry weight using a ratio between the wet and dry weight of 0.25 (Oshima et al. [27]). The C/N ratio determined for eelgrass in 2006 was applied to the eelgrass material.

3. Model Description

The ecosystem model was developed by coupling a physical model with a bio-chemical model. The physical model used a three-dimensional numerical ocean model, the Princeton Ocean Model (Mellor [23]), adding atmospheric, riverine and tidal forcings. The computational domain of the ecosystem model included both Akkeshi Lake and Akkeshi Bay (Figure 1 (a)). The horizontal resolution was $500\text{m} \times 500\text{m},$ with four uniform vertical sigma layers, and the grid was discretized by 42×23 horizontal points. The external (two-dimensional) and internal (three-

dimensional) time steps were 1 second and 30 seconds, respectively. The model was run for nine months from April to December 2007, thus representing the entire year, except during the ice-cover season. For model stabilization, the month of April was run twice.

The biochemical model was based on the model described by Oshima et al. [26]. However, while these previous investigators ran their model only for one month, we ran the model for nine months. The biochemical process is shown schematically in Figure 2. The biochemical compartments used in the present study are as follows:

- Phytoplankton (PHY)

- Zooplankton (ZOO)

- Dissolved Inorganic Matter (DIM), as:

    Ammonium (NH_4)

    Nitrate (NO_3)

    Phosphate (PO_4)

- Dissolved Organic Matter (DOM), as:

    Dissolved Organic Nitrogen (DON)

    Dissolved Organic Phosphorus (DOP)

- Particulate Organic Matter (POM), as:

    Particulate Organic Nitrogen (PON)

    Particulate Organic Phosphorus (POP)

- Eelgrass (EEL)

- Epiphytic algae (EPI)

- Oyster (OYS)

- Manila clam (MC)

The parentheses represent state variables for each compartment, while the arrows represent the fluxes of nitrogen and/or phosphorus between and among the state variables (Figure 2). The formulations of equations are same as those reported in Oshima et al. [26], except for eelgrass and epiphytic algae. Therefore, in the

present study, we omitted equations and parameter values for phytoplankton, zooplankton, DIM, DOM, POM, oysters and the Manila clam. Components and equations that are different from Oshima et al. [26] (i.e., eelgrass and epiphytic algae) are described below, and the parameter values used in this study are provided in Table 1.

Additionally, to estimate the POM fluxes classified by source, we separated POM into eight classes according to its sources, as shown in Figure 3. The POM classes subdivided by source are given as:

- POMeel: particulate organic matter derived from eelgrass

- POMepi: particulate organic matter derived from epiphytic algae

- POMoys: particulate organic matter derived from oyster

- POMmc: particulate organic matter derived from the Manila clam

- POMphy: particulate organic matter derived from phytoplankton

- POMzoo: particulate organic matter derived from zooplankton

- POMout: particulate organic matter from outside the estuary (i.e., open sea)

- POMriv: particulate organic matter from the river

The formulations for each POM class are as follows. In all of the formulations given below, the physical terms of diffusion and advection are omitted for simplicity.

$$\frac{d(POMeel)}{dt} = \text{(Mortality of EEL)} - \text{(Ingestion of POMeel by OYS)}$$
$$- \text{(Decomposition of POMeel into DIM)} - \text{(Decomposition of POMeel into DOM)} - \text{(Settling of POMeel)}$$

$$\frac{d(POMepi)}{dt} = \text{(Mortality of EPI)} - \text{(Ingestion of POMepi by OYS)}$$
$$- \text{(Decomposition of POMepi into DIM)} - \text{(Decomposition of POMepi into DOM)} - \text{(Settling of POMepi)}$$

$$\frac{d(POMoys)}{dt} = \text{(Egestion of OYS)} - \text{(Ingestion of POMoys by OYS)}$$
$$- \text{(Decomposition of POMoys into DIM)} - \text{(Decomposition of POMoys into DOM)} - \text{(Settling of POMoys)}$$

$$\frac{d(POMmc)}{dt} = \text{(Egestion by MC)} - \text{(Ingestion of POMmc by OYS)}$$
$$- \text{(Decomposition of POMmc into DIM)} - \text{(Decomposition of}$$
$$\text{POMmc into DOM)} - \text{(Settling of POMmc)}$$

$$\frac{d(POMphy)}{dt} = \text{(Mortality of PHY)} - \text{(Ingestion of POMphy by OYS)}$$
$$- \text{(Decomposition of POMphy into DIM)} - \text{(Decomposition of}$$
$$\text{POMphy into DOM)} - \text{(Settling of POMphy)}$$

$$\frac{d(POMzoo)}{dt} = \text{(Mortality of ZOO)} + \text{(Egestion by ZOO)} - \text{(Ingestion of POMzoo}$$
$$\text{by OYS)} - \text{(Decomposition of POMzoo into DIM)}$$
$$- \text{(Decomposition of POMzoo into DOM)} - \text{(Settling of POMzoo)}$$

$$\frac{d(POMout)}{dt} = - \text{(Ingestion of POMout by OYS)} - \text{(Decomposition of POMout into}$$
$$\text{DIM)} - \text{(Decomposition of POMout into DOM)} - \text{(Settling of}$$
$$\text{POMout)}$$

$$\frac{d(POMriv)}{dt} = - \text{(Ingestion of POMriv by OYS)} - \text{(Decomposition of POMriv into}$$
$$\text{DIM)} - \text{(Decomposition of POMriv into DOM)} - \text{(Settling of}$$
$$\text{POMriv)}$$

The decomposition of POM was assumed to be proportional to POM concentration with a Q10 relation, and the settling of POM was assumed to be proportional to POM concentration with settling velocity (Kawamiya et al. [19]; Oshima et al. [27]; Oshima et al. [26]).

$$\text{(Decomposition of POM into DIM)} = POMDIM0 \times \exp(Kpomdim \times T) \times POM$$

$$\text{(Decomposition from POM into DOM)} = POMDOM0 \times \exp(Kpomdom \times T)$$
$$\times POM$$

$$\text{(Settling of POM)} = \frac{\partial}{\partial z}(VsetPOM \times POM),$$

where POMDIM0 (day^{-1}) is the decomposition rate from POM into DIM at 0°C, POMDOM0 (day^{-1}) is the decomposition rate from POM into DOM at 0°C,

Kpomdim (°C^{-1}) is temperature coefficient for decomposition from POM into DIM, Kpomdom (°C^{-1}) is temperature coefficient for decomposition from POM into DOM, T (°C) is water temperature, $z\,(m)$ is depth at any layer, and VsetPOM is the settling velocity of POM. We assumed that the decomposition rate and the settling velocity of all sources have the same values.

The biochemical processes included in this model are based on nitrogen and phosphorus flows. To estimate POC, we converted PON, which is calculated by means of this expanded ecosystem model, into POC using the ratio between POC and PON. The conversion rates among carbon, nitrogen, phosphorus and biomass for each compartment are shown in Table 2, together with the associated references.

3.1. Sub-model for eelgrass and associated epiphytic algae

An eelgrass plant consists of both aboveground portions (leaves and stems) and belowground portions (roots and rhizomes). The production of aboveground portions consists of the primary production and the transfer of material from belowground portions. However, in this study, only the aboveground portion of the eelgrass was considered because our model does not include the benthic ecosystem. Therefore, we assumed the biomass of eelgrass as an external forcing. The biomass is given based on observation data from station L2 (Figure 4) and is assumed to be uniform in the area indicated in Figure 1(b). We also assumed the biomass is vertically constant to convert the biomass per square meter into the biomass per liter. Thus, the biomass can be divided by depth. Furthermore, the carbon-nitrogen content in eelgrass was observed monthly and is shown in Table 2. Based on the results presented in Table 2, we used time-dependent values of the C/N ratio for POM derived from eelgrass (POMeel) by interpolating these values.

In the model, the processes of eelgrass were separated into three parts as: photosynthesis, respiration and mortality. The photosynthesis of eelgrass was estimated as the nutrient uptake by the leaves obtained from Short and McRoy [30] and Stapel et al. [31]. The processes associated with photosynthesis in the model represent the nitrogen flow $(\mu\text{molN}\,1^{-1}\text{day}^{-1})$ and phosphorus flow $(\mu\text{molP}\,1^{-1}\text{day}^{-1})$.

Nitrogen flow

(Photosynthesis of EEL) = (Ammonium uptake of EEL) + (Nitrate uptake of EEL)

Phosphorus flow

(Photosynthesis of EEL) = (Phosphate uptake of EEL)

Equations for individual processes are as follows:

(Ammonium uptake of EEL)

$$= \text{VmaxNH4EEL} \times \frac{\text{NH}_4}{\text{NH}_4 + \text{Knh4EEL}} \times \frac{\text{EEL}}{\text{DEP}} \times \text{LtoM3}$$

(Nitrate uptake of EEL)

$$= (\text{Ammonium uptake of EEL}) \times \frac{\text{Ano3} \times \text{NO}_3 + \text{Bno3}}{\text{Anh4} \times \text{NH}_4 + \text{Bnh4}}$$

(Phosphate uptake of EEL)

$$= \text{VmaxPO4EEL} \times \frac{\text{PO}_4 - \text{SminPO4}}{\text{PO}_4 - \text{SminPO4} + \text{Kpo4EEL}} \times \frac{\text{EEL}}{\text{DEP}} \times \text{LtoM3},$$

where $\text{EEL}\,(\text{gDW m}^{-2})$ is the eelgrass biomass measured in gDW per square meter (DW means dry weight), DEP (m) is water depth, and LtoM3 $(= 10^{-3}\,\text{m}^3\text{l}^{-1})$ is a conversion coefficient. Please refer to Table 1 for parameters not mentioned here.

The respiration of eelgrass was determined based on the method of Bach [3]. The mortality of eelgrass was divided into two parts: natural mortality and shedding of leaves (Behm et al. [5]). The shedding of leaves was assumed to occur in late summer/fall (Josselyn and Mathieson [18]). The loss due to the consumption by swans was not accounted for in the model. Natural mortality was proportional to the biomass of eelgrass with a Q10 relationship, and the loss through the shedding of leaves was forced by a seasonal litterfall index. The processes associated with respiration and mortality represent nitrogen flow $(\mu\text{molN}\,\text{l}^{-1}\text{day}^{-1})$ in this text, and the processes can be converted into phosphorus flow $(\mu\text{molP}\,\text{l}^{-1}\text{day}^{-1})$ in the model using the nitrogen-phosphorus ratio (Table 2).

(Respiration of EEL)

$$= \text{Res20EEL} \times \text{KresEEL}^{(T-20)} \times \frac{\text{EEL}}{\text{DEP}} \times \text{LtoM3} \times \text{RndwEEL} \times \text{MCR},$$

where Res20EEL (day^{-1}) is the maximum respiration rate at 20°C, KresEEL (day^{-1}) is the temperature coefficient for respiration, RndwEEL is the ratio between nitrogen and the dry weight of eelgrass, and MCR $(= 10^6 \mu\text{g g}^{-1})$ is the conversion coefficient.

$$\text{(Mortality of EEL)}$$

$$= \{\text{Mor0EEL} \times \exp(\text{KmorEEL} \times T) + \text{LitEEL} \times (\text{Litterfall Index})\}$$

$$\times \frac{\text{EEL}}{\text{DEP}} \times \text{LtoM3} \times \text{RndwEEL} \times \text{MCR},$$

where Mor0EEL (day^{-1}) is the mortality rate at 0°C, KmorEEL $(°\text{C}^{-1})$ is the temperature coefficient for mortality, LitEEL (day^{-1}) is the maximum litterfall rate, and the Litterfall Index (no dimension) is calculated as:

$$\text{(Litterfall Index)} = \exp\left\{-0.5\left(\frac{\text{time} - 167}{20.447}\right)^2\right\},$$

where time (day) is zero for April 1st, which was the first day of the model's run, and it is 274 on December 31th, the end day of the run.

The processes related to epiphytic algae were divided into four parts: photosynthesis, respiration, extracellular excretion and mortality. The model did not take into account grazing by consumers or suspension of epiphytic algae due to external factors. The biomass of epiphytic algae was derived from observations (Figure 4). The processes of photosynthesis, respiration and extracellular excretion of epiphytic algae were calculated with the same formulation as used for phytoplankton (Oshima et al. [27]; Oshima et al. [26]). The mortality of epiphytic algae was assumed to be a function of eelgrass mortality (i.e., natural mortality and the shedding of leaves) and the ratio between epiphytic algae and eelgrass biomass (Buzzelli et al. [6]).

3.2. Initial, boundary and forcing conditions

The initial and open boundary condition used in the present study is shown in Table 3. For the open boundary condition of water temperature, we estimated the second order regression function based on observation data from 2007 (Akkeshi Fisheries Cooperative Association [1]) as:

$$T_{open} = -0.0007 \times time^2 + 0.1950 \times time + 4.0724,$$

where T_{open} (°C) is the water temperature at the open boundary. The salinity for the open boundary condition was fixed at 30.5 (surface layer) to 32.5 (bottom layer).

The open boundary condition of the ecological compartments was basically determined by interpolating monthly observation data in Akkeshi Bay from 2006 (Table 3). For atmospheric forcing, daily mean data (or daily total data) from AMeDAS (JMA [17]) for April to December 2007 were used (Table 4). For river forcing, the Bekanbeushi River discharge and water temperature were estimated using the equations suggested by Krasnenko et al. [22] for the Akkeshi estuary due to an absence of available observation data.

$$RD = 0.335 \times Pr + 14.57$$

$$T_{river} = 0.860 \times T_{air} + 2.963,$$

where RD $(m^3\,sec^{-1})$ is the river discharge, Pr $(mm\,week^{-1})$ is the cumulative precipitation for one week, T_{river} (°C) is the river water temperature, and T_{air} (°C) is the mean air temperature for one week. Nutrients and POM were obtained from measurements carried out at the Bekanbeushi River (station R1) in 2007 (Table 4). Surface elevation was calculated using four tidal components $(M_2, S_2, K_1$ and $O_1)$ as tidal forcing at the open boundary (Table 4).

In the present study, the model was run under the atmospheric, riverine, tidal (tidal level) and open boundary conditions in 2007, when water sampling was conducted at the Bekanbeushi River, from which the river discharge contributes greatly to Akkeshi Lake (Iizumi et al. [15] and Iizumi et al. [14]). Although the monitoring of eelgrass and epiphytic algae was carried out in 2006, we assumed that there were no significant differences in the eelgrass and epiphytic algae biomass between 2006, 2007 and 2008.

4. Results and Discussion

4.1. Model validation

A comparison of the model results for chlorophyll a, PON, nitrate and phosphate with the observation data for Akkeshi Lake from 2007 is shown in Figure 5. The model results are vertically averaged daily mean values. The chlorophyll a

values show good agreement with the observation data, except in summer and winter, when the observed value is higher than the model values (Figure 5(a)). The high concentration of chlorophyll a is similar with the high biomass of epiphytic algae (Figure 4). In this study, the chlorophyll a was calculated as only phytoplankton because the model did not take into account suspension of epiphytic algae. Thus, the chlorophyll a was underestimated due to ignore the suspension of epiphytic algae. The PON values shown in Figure 5(b) represent an aggregation of the POC values classified by sources. The PON values are associated with large gaps between the observation and model results at the center and throughout the inner region of the lake (stations L2 and L3) in the litterfall season. This is attributed to the removal of eelgrass leaves during sampling. The nutrient values from the model show good agreement with the observation data, although the modeled phosphate concentration was lower than was observed in summer (Figure 5(d)).

4.2. Time-dependent characteristics of POC

The time-dependent characteristics of POC subdivided into different sources at the mouth of Akkeshi Lake (station L4) between April and December in 2007 are shown in Figure 6. The model results are vertically averaged daily mean values. POC derived from eelgrass and associated epiphytic algae (POCeel + POCepi) begins to increase from the middle of May due to the growth of these organisms and increases more rapidly from the middle of July because of the litterfall of eelgrass, though the biomass of eelgrass decreases (Figure 4). After the litterfall season, POCeel + POCepi decreases with the biomass of eelgrass. POC from oysters and the Manila clam (POCoys + POCmc) shows the lowest concentration, despite the fact that these species are actively cultured in Akkeshi Lake. POC derived from phytoplankton and zooplankton (POCphy + POCzoo) shows levels that are approximately two times higher in summer than in spring and fall, though the value of this parameter is not large. POC from outside (i.e., the open sea) and river (POCout + POCriv) shows a slowly decreasing trend from spring to winter (refer to Table 3 and Table 4). Therefore, eelgrass and epiphytic algae are the most important sources of POC in Akkeshi Lake, especially in the litterfall season.

4.3. Horizontal distribution of POC

In Figure 6, it can be seen that POC shows the highest concentration in September. The horizontal distributions of POC subdivided by its sources at the surface layer are shown in Figure 7. The model results are expressed as monthly mean values. The horizontal distribution of POC is characterized by the horizontal

distribution of eelgrass, oysters and the Manila clam (Figure 1(b)); the current velocity (not shown); the river inflow and the open boundary condition. POC from eelgrass and epiphytic algae (POCeel + POCepi) exhibits a particularly high concentration, above 1000 $\mu gC1^{-1}$, in the lake due to eelgrass litterfall (Figure 8(a)). This has a considerable effect not only in the lake but also in the bay. In the bay, the amount of POC from eelgrass and epiphytic algae (POCeel + POCepi) is greater than POC from plankton (POCphy + POCzoo) (Figure 8(c)). The distribution of POC from shellfishes corresponds to the habitats of these species (Figure 8(b)). POC from plankton (POCphy + POCzoo) is associated with a higher concentration in the southeastern region of the lake, where eelgrass is not distributed (Figure 8(c)). Although the river contributes strongly to the lake (Iizumi et al. [15] and Iizumi et al. [14]), it does not extend to the inner regions of the lake due to current characteristics (Figure 8(d)).

4.4. Inflow and outflow of POC derived from eelgrass and epiphytic algae

Comparisons between the observation data and the model results for the inflow and outflow fluxes of POC derived from eelgrass and epiphytic algae (POCeel + POCepi) at the mouth of Akkeshi Lake (station L4) on August 15th and September 17th, 2007, are shown in Figure 9(a) and (b), respectively. The positive values indicate inflow to the lake, while negative values indicate outflow from the lake. As previously mentioned, our model was simulated in 2007, but the observations were carried out only in 2008. Therefore, we adjusted the tidal phase between 2007 and 2008 as follows: Figure 9(c) and (d) show the tidal phase and level of both years (JMA, 2007, 2008), and as shown by arrows, the dates for 2007 were shifted by 70 hours to adjust the tidal phase. Consequently, in Figure 9(a) and (b), the observations conducted from 4:00 to 16:00 on August 18th (spring tide) and September 20th (neap tide) in 2008 correspond to the modeled results from 6:00 to 18:00 on August 15th and September 17th in 2007, respectively.

The inflow and outflow of POC depend on the tidal current, such that POC flows into the lake from the bay during flood flows and out of the lake during ebb flows. This phase in the model shows good agreement with the observation data, except at 7:00 on August 15th, when the observed value is higher than the model value, regardless of the tidal current (Figure 9(a)). This is most likely due to hourly changes in wind which could not be simulated because only the daily mean wind speed and prevailing wind direction were used in the model (Table 4).

The magnitude of inflow and outflow flux is greater during spring tide than in neap tide due to current velocity. The inflow and outflow quantities can be represented as the signed area of the region bounded by the graph of flux. As in the observation data, the inflow is 11kgC m^{-2} during spring tide (August) and 3kgC m^{-2} during neap tide (September) for a period of 12 hours (6:00 to 18:00), and the outflow is 15kgC m^{-2} and 8kgC m^{-2}, respectively. However, the model results show that the inflow is 14kgC m^{-2} and 4kgC m^{-2}, and the outflow is 24kgC m^{-2} and 9kgC m^{-2}, respectively. Generally the model values are higher than the observed values. Since the lake is really shallow and the sediment is silt and clay (Hasegawa et al. [11]), a lot of the eelgrass biomass become buried in the sediments of the lake and not advected from the sediments. However, in the model, the biomass per square meter was divided by depth and converted into the biomass per liter. Thus, advectable POCeel + POCepi were overestimated.

4.5. POC flux

The daily inflow/outflow flux of POC can be calculated as the total inflow and outflow flux in a day. Figure 9 shows the time-dependent characteristics of the inflow and outflow flux of POC according to its sources between April and December, 2007. The model results are vertically integrated daily values. The positive values indicate inflow to the lake, while the negative values indicate outflow from the lake. According to its sources, POC derived from eelgrass and epiphytic algae (POCeel + POCepi) and from oysters and the Manila clam (POCoys + POCmc) flows out from the lake for the nine modeled months (inflow << outflow), while POC from phytoplankton and zooplankton (POCphy + POCzoo) and from outside and river sources (POCout + POCriv) flows into the lake (inflow > outflow). As shown in Figure 6, POC derived from eelgrass and epiphytic algae (POCeel + POCepi) is a major component of total POC and its outflow also exhibits the same characteristics as a main compartment of the inflow/outflow of POC. The outflow flux exhibits a 15-day period corresponding to the tidal phase and is associated with a maximum during spring tide and a minimum during neap tide, although the monthly trend of the outflow flux is proportional to the POC concentration in the lake (Figure 6).

The inflow/outflow quantity of POC according to its sources at the mouth of Akkeshi Lake and the production of POC in the lake during nine months from April to December in 2007 are shown in Table 5. The total POC inflow/outflow quantities

to/from Akkeshi Lake during nine months from April to December is –4648 tons; according to its sources, –4414 tons (outflow) are from eelgrass and epiphytic algae (POCeel + POCepi); –551 tons (outflow) come from oysters and the Manila clam (POCoys + POCmc); 145 tons (inflow) are associated with phytoplankton and zooplankton (POCphy + POCzoo); 383 tons (inflow) come from outside (POCout); and –211 tons (outflow) are from river (POCriv). The total POC production is approximately 75727 tons, 89% of which is from eelgrass and epiphytic algae; 7 % is from oysters and the Manila clam; 3% is from phytoplankton and zooplankton; and 1% comes from river. This indicates that the main source of the POC produced in the lake is eelgrass and epiphytic algae. Of the total POC produced in Akkeshi Lake, 6% (4648 tons) flows out to Akkeshi Bay. Furthermore, 35% (26578 tons) of the POC produced in the lake decomposes into dissolved carbon, and 27% (20326 tons) settles to the bottom.

5. Conclusions

To estimate the particulate organic carbon (POC) flux associated with various sources, including eelgrass, flowing out from Akkeshi Lake to Akkeshi Bay, which is a subarctic estuary of Hokkaido, Japan, and to evaluate the role of eelgrass in carbon transport, we developed an ecosystem model that includes phytoplankton, zooplankton, dissolved inorganic matter (DIM), dissolved organic matter (DOM), particulate organic matter (POM), eelgrass, epiphytic algae, oysters and the Manila clam. The model results show good agreement with observation data for the computational period. Eelgrass and epiphytic algae are the most important sources of POC in Akkeshi Lake, especially in the litterfall season. The total POC inflow/outflow quantities to/from Akkeshi Lake during nine months from April to December is –4648 tons; according to its sources, –4414 tons (outflow) are from eelgrass and epiphytic algae; –551 tons (outflow) are associated with from oysters and the Manila clam; 145 tons (inflow) are from phytoplankton and zooplankton; 383 tons (inflow) come from outside (i.e., open sea); and –211 tons (outflow) are from river. The total POC production in the lake is approximately 75727 tons; 89% is from eelgrass and epiphytic algae; 7% is from oysters and the Manila clam; 3% is from phytoplankton and zooplankton; and 1% is from river. This indicates that the main source of the POC produced in the lake is eelgrass and epiphytic algae. Of the POC produced in Akkeshi Lake, 6% (4648 tons) flows out to Akkeshi Bay. Furthermore, 35% (26578 tons) of the POC produced in the lake decomposes into dissolved carbon, and 27% (20326 tons) settles to the bottom.

Acknowledgements

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Table 1. Parameters of biochemical model

Symbol	Description	Unit	Value
Parameters for eelgrass (EEL)			
VmaxNH4EEL	Maximum ammonium uptake rate of eelgrass	$\mu mo1NgDW^{-1}day^{-1}$	832
Knh4EEL	Eelgrass half saturation constant for ammonium	$\mu mo1N1^{-1}$	36.33
Ano3	Nitrate uptake coefficient of eelgrass	$gDW^{-1}day^{-1}$	11.28
Bno3	Nitrate uptake constant of eelgrass	$\mu mo1NgDW^{-1}day^{-1}$	20.16
Anh4	Ammonium uptake coefficient of eelgrass	$gDW^{-1}day^{-1}$	19.2
Bnh4	Ammonium uptake constant of eelgrass	$\mu mo1NgDW^{-1}day^{-1}$	21.36
VmaxPO4EEL	Maximum phosphate uptake rate of eelgrass	$\mu mo1PgDW^{-1}day^{-1}$	63.2
Kpo4EEL	Eelgrass half saturation constant for phosphate	$\mu mo1P1^{-1}$	11.23
SminPO4EEL	Minimum concentration for phosphate uptake	$\mu mo1P1^{-1}$	0.91
Res20EEL	Eelgrass maximum respiration rate at 20°C	day^{-1}	0.014
KresEEL	Eelgrass temperature coefficient for respiration	day^{-1}	1.07
Mor0EEL	Eelgrass mortality rate at 0°C	day^{-1}	0.0001
KmorEEL	Eelgrass temperature coefficient for mortality	$°C^{-1}$	0.0693
LitEEL	Maximum litterfall rate	day^{-1}	0.0540
Parameters for epiphytic algae (EPI)			
VmaxEPI	Maximum photosynthetic rate of epiphytic algae at 0°C	day^{-1}	0.1
Knh4EPI	Epiphytic algae half saturation constant for ammonium	$\mu molN1^{-1}$	1
Kno3EPI	Epiphytic algae half saturation constant for nitrate	$\mu molN1^{-1}$	3
Kpo4EPI	Epiphytic algae half saturation constant for phosphate	$\mu mo1P1^{-1}$	0.1
PusaiEPI	Epiphytic algae ammonium inhibition coefficient	$1\mu mo1N^{-1}$	1.462
KgppEPI	Temperature coefficient for epiphytic algae photosynthetic rate	$°C^{-1}$	0.0693
IoptEPI	Optimal light intensity of epiphytic algae	$ly\ day^{-1}$	288
Res0EPI	Epiphytic algae respiration rate at 0°C	day^{-1}	0.003
KresEPI	Temperature coefficient for epiphytic algae respiration	$°C^{-1}$	0.0519
GammaEPI	Ratio of extracellular excretion to photosynthesis of epiphytic algae	No dim	0.135

Parameters for decomposition of organisms

POMDIM0	Decomposition rate from POM to DIM at 0°C	day^{-1}	0.01
Kpomdim	Temperature coefficient for decomposition from POM to DIM	°C^{-1}	0.0693
POMDON0	Decomposition rate from POM to DOM at 0°C	day^{-1}	0.01
Kpomdom	Temperature coefficient for decomposition from POM to DOM	°C^{-1}	0.0693

Parameters for settling

VsetPOM	Settling velocity of POM	m day^{-1}	0.3

Table 2. Element content of all compartments and the ratio between POC and PON used in the present study

Compartment	Chlorophyll a (gChl.a)	Carbon (gC)	Nitrogen (gN)	Phosphorus (gP)	References		POM	POC/PON (molC/molN)
Phytoplankton	1	50	-	-	Kawamiya et al. [19]		POMphy	6.97
	-	108[1]	15.5[2]	1[3]	Redfield ratio			
Zooplankton	-	103[1]	16.5[2]	1[3]	Redfield ratio		POMzoo	6.24
Eelgrass	1[4]	0.3578	0.0227	-	Apr	Observation data (2006)	POMeel	18.38
		0.3512	0.0228		May			17.94
		0.3426	0.0134		Jun			29.72
		0.3366	0.0108		Jul			36.44
		0.3315	0.0088		Aug			43.88
		0.3423	0.0202		Sep			19.77
		0.3585	0.0196		Oct			21.34
		0.3474	0.0207		Nov			19.58
		0.3516	0.0261		Dec			15.73
	-	-	18	1	Atkinson and Smith [2]			
Epiphytic algae	1	43	-	-	Hasegawa et al. [10]		POMepi	10.97
	-	9.4	1	-				
	-	-	15.5[2]	1[3]	Redfield ratio			
Oyster	1[4]	0.5	0.088	0.011	Cerco and Noel [7]		POMoys	6.63
Manila clam	1[4]	0.377	0.117	0.01	Nizzoli et al. [25]		POMmc	3.76
-	-	-	-	-	Observation data (2006)		POMout	7.25
-	-	-	-	-	Observation data (2007)		POMriv	9.62

(1) molC

(2) molN

(3) molP

(4) tissue dry weight (gDW)

Table 3. Initial and open boundary condition of water temperature, salinity and compartments for the biochemical model

Initial condition						
Compartment	Unit		1st layer	2nd layer	3rd layer	4th layer
W. Temp.	°C		7.1	7.1	7.1	7.1
Salinity	-		30.5	31.0	31.5	32.0
PHY	μgChl.a1^{-1}		1.0	1.0	1.0	1.0
ZOO	μmo1C1^{-1}		1.0	1.0	1.0	1.0
NH_4	μmo1N1^{-1}		1.0	1.0	1.0	1.0
NO_3	μmo1N1^{-1}		1.0	1.0	1.0	1.0
PO_4	μmo1P1^{-1}		0.1	0.1	0.1	0.1
DON	μmo1N1^{-1}		1.0	1.0	1.0	1.0
DOP	μmo1P1^{-1}		0.1	0.1	0.1	0.1
PON[1]	μmo1N1^{-1}		1.0	1.0	1.0	1.0
POP[1]	μmo1P1^{-1}		0.1	0.1	0.1	0.1
	Density (ind m^{-2})		Dry weight (gDW ind^{-1})		Biomass (gDW m^{-2})	
EEL	-		-		36.5[2]	
EPI	-		-		36.0[2]	
OYS[3]	-		-		0.0074[4]	
MC[3]	3200		0.15		480	

Open boundary condition											
Compartment	Unit	Layer	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
W. Temp.	°C	All	Calculated								
Salinity	No dim	1st	30.5	30.5	30.5	30.5	30.5	30.5	30.5	30.5	30.5
		2nd	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0	31.0
		3rd	31.5	31.5	31.5	31.5	31.5	31.5	31.5	31.5	31.5
		4th	32.5	32.5	32.5	32.5	32.5	32.5	32.5	32.5	32.5
PHY[2]	μgChl.a1^{-1}	1st	5.60	2.65	4.68	2.25	2.06	3.45	3.39	1.45	1.53
		2nd	7.28	5.31	7.06	5.28	2.43	3.35	3.20	1.43	1.63
		3rd	8.96	7.96	9.44	8.30	2.79	3.24	3.00	1.41	1.74
		4th	10.64	10.62	11.82	11.33	3.16	3.14	2.81	1.39	1.84
DON[3]	μmo1N1^{-1}	All	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00

$DOP^{(3)}$	$\mu mol P l^{-1}$	All	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30
$NH_4^{(2)}$	$\mu mol N l^{-1}$	1st	2.20	1.60	1.60	1.20	1.20	1.00	1.00	1.40	1.40
		2nd	2.00	1.40	1.40	1.00	1.00	0.80	0.80	1.20	1.20
		3rd	1.80	1.20	1.20	0.80	0.80	0.60	0.60	1.00	1.00
		4th	1.60	1.00	1.00	0.60	0.60	0.40	0.40	0.80	0.80
$NO_3^{(2)}$	$\mu mol N l^{-1}$	1st	0.87	0.16	0.07	0.21	0.12	1.37	6.67	9.43	8.54
		2nd	0.95	0.56	0.98	1.26	0.24	1.59	7.16	9.29	8.59
		3rd	1.04	0.96	1.90	2.31	0.37	1.81	7.66	9.14	8.63
		4th	1.12	1.36	2.81	3.36	0.49	2.03	8.15	9.00	8.68
$PO_4^{(2)}$	$\mu mol P l^{-1}$	1st	0.47	0.33	0.36	0.68	0.24	0.75	1.11	1.14	1.11
		2nd	0.56	0.39	0.48	0.74	0.31	0.82	1.20	1.20	1.13
		3rd	0.64	0.46	0.61	0.80	0.37	0.88	1.29	1.27	1.16
		4th	0.73	0.52	0.73	0.86	0.44	0.95	1.38	1.33	1.18
$PON^{(1)(2)}$	$\mu mol N l^{-1}$	1st	4.69	3.69	5.49	3.89	3.13	6.05	3.09	1.96	2.90
		2nd	6.21	4.42	6.00	4.90	3.45	6.18	3.42	2.30	3.30
		3rd	7.72	5.14	6.52	5.90	3.76	6.30	3.75	2.64	3.71
		4th	9.24	5.87	7.03	6.91	4.08	6.43	4.08	2.98	4.11
$POP^{(1)(5)}$	$\mu mol P l^{-1}$	1st	0.47	0.37	0.55	0.39	0.31	0.61	0.31	0.20	0.29
		2nd	0.62	0.44	0.60	0.49	0.34	0.62	0.34	0.23	0.33
		3rd	0.77	0.51	0.65	0.59	0.38	0.63	0.38	0.26	0.37
		4th	0.92	0.59	0.70	0.69	0.41	0.64	0.41	0.30	0.41
$ZOO^{(2)}$	$\mu mol C l^{-1}$	All	1.54	1.17	2.33	6.48	2.87	5.88	1.08	1.11	0.36

(1) POM means POMout.

(2) Observation data (2006)

(3) Oshima et al. [26]

(4) gWW (g wet weight)

(5) PON/POP ratio = 10 : 1 (Oshima et al. [26])

Table 4. Atmospheric, river and tidal forcing conditions

Parameter		Value								Unit	Reference
Atmospheric forcing conditions											
Wind	Speed	Daily mean data at Ohta[1]								m sec^{-1}	AMeDAS (JMA) [17]
	Direction	Daily most frequent data at Ohta[1]								non-dim (1-16)	
Air temperature		Daily mean data at Ohta[1]								°C	AMeDAS (JMA) [17]
Precipitation		Daily total data at Ohta[1]								mm	AMeDAS (JMA) [17]
Solar radiation		Daily total data at Nemuro[2]								MJ m^{-2} day^{-1}	AMeDAS (JMA) [17]
Relative humidity		Daily mean data at Kushiro[3]								%	AMeDAS (JMA) [17]
Cloud cover		Daily mean data at Kushiro[3]								non-dim (0-10)	AMeDAS (JMA) [17]
Day length		Daily total data at Nemuro[2]								hour	NAOJ [24]
River forcing conditions											
Discharge		Calculated								m^3 sec^{-1}	Krasnenko et al. [22]
Water temperature		Calculated								°C	
Salinity		0								psu	
Biochemical compartment		Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
NH$_4$[4] (μmolN l^{-1})		5.54	2.27	0.01	0.11	2.42	0.39	1.97	1.97	1.97	
NO$_3$[4] (μmolN l^{-1})		10.65	5.12	11.15	0.91	15.15	10.39	10.37	18.28	22.31	
PO$_4$[4] (μmolP l^{-1})		0.66	0.77	0.92	0.51	1.02	0.87	0.70	0.61	0.75	
PON[4][5] (μmolN l^{-1})		9.73	6.59	4.89	10.76	3.87	6.59	4.08	4.85	2.32	
POP[5][6] (μmolP l^{-1})		0.97	0.66	0.49	1.08	0.39	0.66	0.41	0.49	0.23	
Tidal forcing conditions											
Tidal component[7]		Amplitude (meter)			Phase (degree)			Period (day)			
M$_2$		0.29			107			0.5175			
S$_2$		0.12			153			0.5			
K$_1$		0.23			166			0.9971			
O$_1$		0.19			138			1.11958			

(1) Ohta (N43°05.4′ E144°46.7′)

(2) Nemuro (N43°19.8′ E145°35.1′)

(3) Kushiro (N42°59.1′ E144°22.6′)

(4) Observation data (2007)

(5) POM means POMriv.

(6) PON/POP ratio = 10 : 1 (Oshima et al. [26])

(7) Japan Coast Guard [16]

Table 5. Inflow/outflow quantity of POC according to its sources at the mouth of Akkeshi Lake and the production in the lake during nine months from April to December in 2007

Sources	Inflow (+) & outflow (-)[1]		Production	
	(ton)	(%)	(ton)	(%)
Eelgrass and epiphytic algae	-4414	95	67284	89
Oyster and the Manila clam	-551	12	5461	7
Phytoplankton and zooplankton	145	-3	2533	3
Outside (i.e., open sea)	383	-8	0	0
River	-211	4	449[2]	1
Total	-4648	100	75727	100

(1) (+) indicates inflow to Akkeshi Lake from Akkeshi Bay, and (-) indicates outflow from the lake to the bay.

(2) Inflow from Bekanbeushi River to Akkeshi Lake.
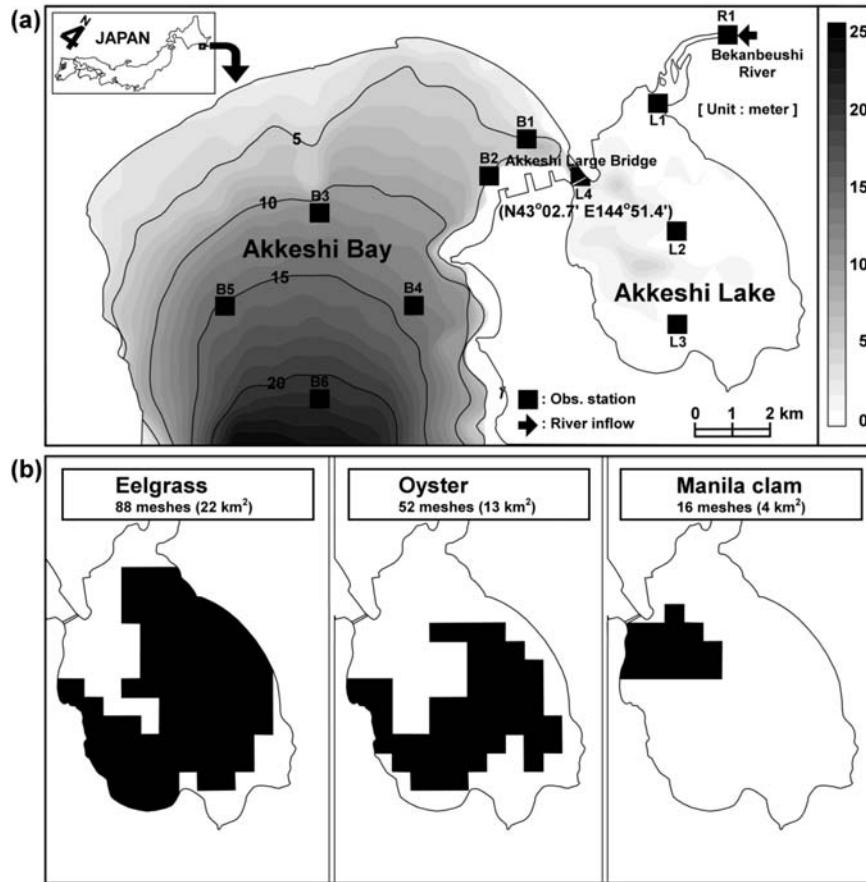
Figure 1. Location of Akkeshi Lake and its bottom topography, together with observation and river inflow points (a) and the distributions of eelgrass and cultured shellfishes (b).
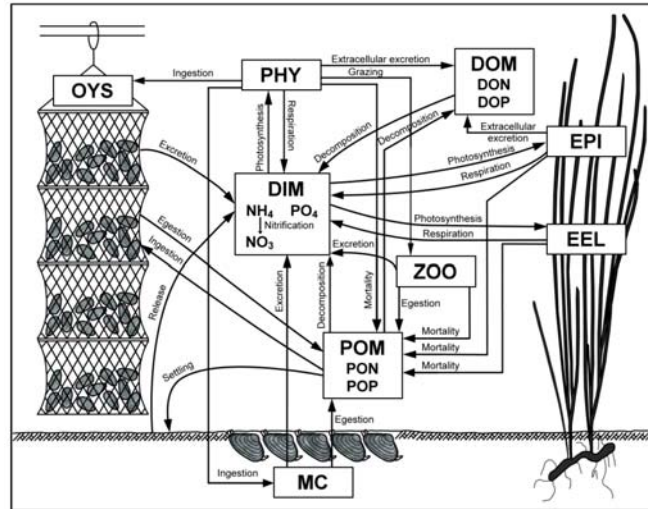
Figure 2. Schematic view of biochemical model.
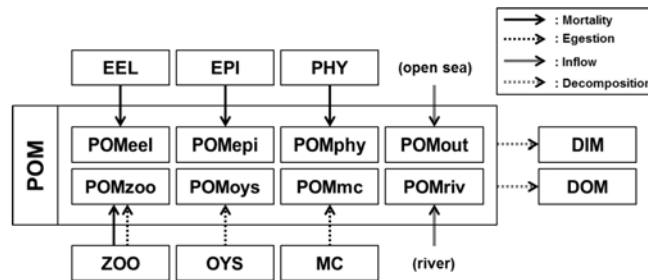
Figure 3. POM subdivisions according to its sources.
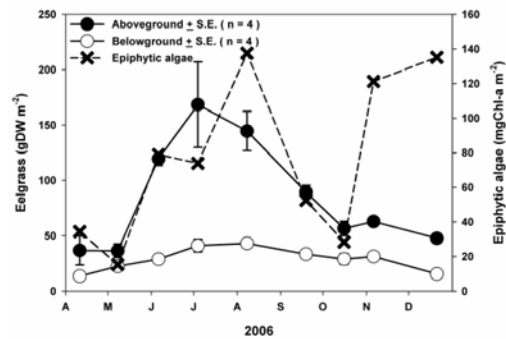
Figure 4. Annual changes in the biomass of eelgrass, Zostera marina, and epiphytic algae at the center of Akkeshi Lake (station L2) in 2006. Vertical bars represent ± S.E. (n = 4).
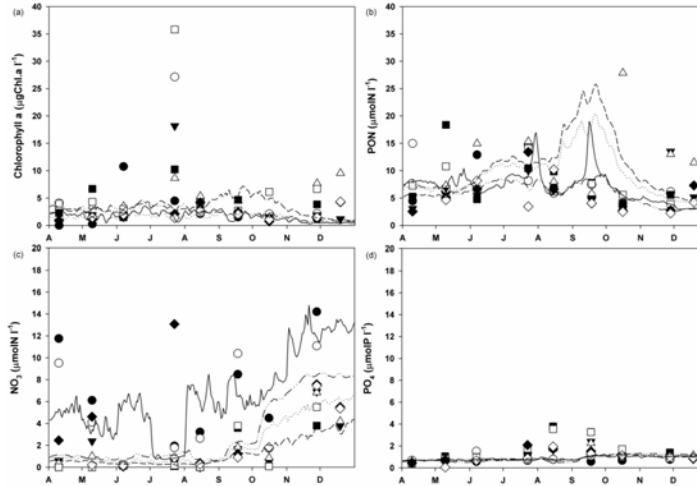
Figure 5. Comparison between observations and model for (a) chlorophyll a, (b) PON, (c) nitrate and (d) phosphate in Akkeshi Lake. Symbols indicate observation data at stations L1 (circle), L2 (triangle), L3 (square) and L4 (diamond) in 2007. Black and white symbols indicate the surface and the bottom, respectively. Lines indicate model results at stations L1 (solid), L2 (dotted), L3 (dash) and L4 (dash-dot-dot).
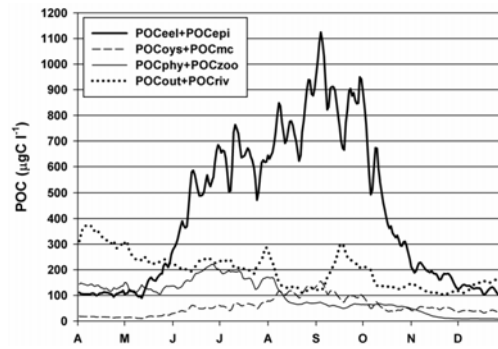
Figure 6. Time-dependent characteristics of each POC class, subdivided into different sources, at the mouth of Akkeshi Lake (station L4) in 2007. Thick solid line: POC derived from eelgrass (POCeel) and associated epiphytic algae (POCepi); dashed line: POC derived from oysters (POCoys) and the Manila clam (POCmc); thin solid line: POC derived from phytoplankton (POCphy) and zooplankton (POCzoo); and dotted line: POC derived from outside (i.e., open sea) (POCout) and river (POCriv).
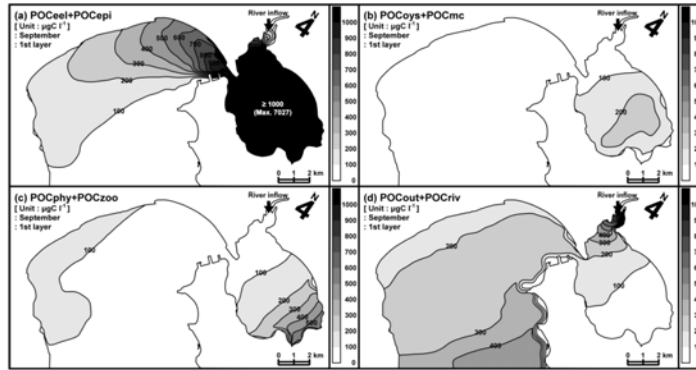
Figure 7. Horizontal distributions of POC subdivided by its sources: (a) eelgrass and epiphytic algae (POCeel + POCeel), (b) oysters and the Manila clam (POCoys + POCmc), (c) phytoplankton and zooplankton (POCphy + POCzoo) and (d) outside and river (POCout + POCriv) at the surface layer of Akkeshi estuary in September 2007.
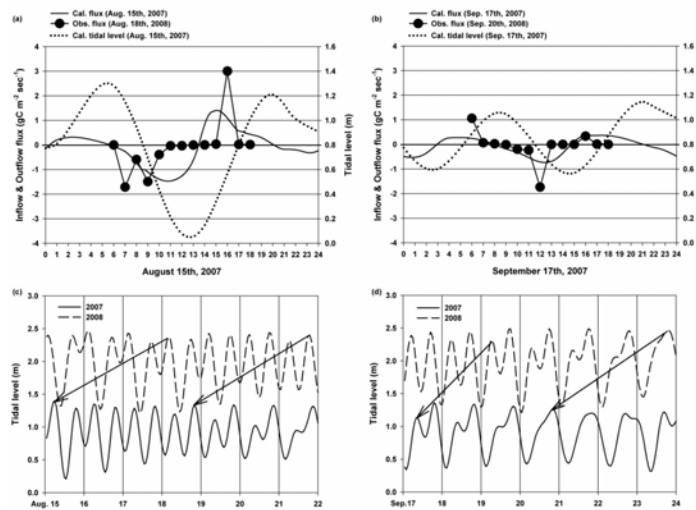

Figure 8. (a) and (b) show a comparison between the observations and model results for the inflow and outflow fluxes of POC derived from eelgrass and epiphytic algae (POCeel + POCepi) at the mouth of Akkeshi Lake (station L4) on August 15th and September 17th 2007, respectively. On the y-axis (+) indicates inflow to the lake, and (-) indicates outflow from the lake. (c) and (d) show a comparison between 2007 and 2008 for the tidal level at Kushiro (JMA, 2007 and 2008) to explain the inconsistency in the dates between the observations and model results.
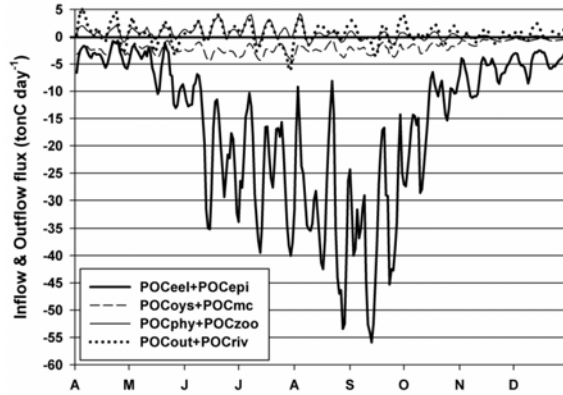
Figure 9. Time-dependent characteristics of the inflow and outflow fluxes of each POC class, subdivided according to its sources, at the mouth of Akkeshi Lake (station L4) between April and December 2007. On the y-axis, (+) indicates inflow to the lake, and (-) indicates outflow from the lake. Thick solid line: POC derived from eelgrass (POCeel) and associated epiphytic algae (POCepi); dashed line: POC derived from oysters (POCoys) and the Manila clam (POCmc); thin solid line: POC derived from phytoplankton (POCphy) and zooplankton (POCzoo); and dotted line: POC derived from outside (i.e., open sea) (POCout) and river (POCriv).