Aquaculture 529 (2020) 735564

Contents lists available at ScienceDirect

Aquaculture

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

# Modeling bottom-up and top-down controls on the low recruitment success of oyster larvae in Hiroshima Bay, Japan

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ARTICLE INFO

*Keywords:*
Ecosystem model
Filter feeder
Oyster
Phosphorus cycle
Prey-predator

ABSTRACT

A measured reduction in the phosphorus load in Hiroshima Bay, Japan, is suspected to be the root cause of the declining success of oyster spat collections and rates of oyster production over the past 30 years. The lack of phosphorus leads to an inadequate abundance of phytoplankton as food sources which, along with competition among various filter feeders, might have generated the poor culture conditions. To understand how prey-predator interactions, including those of cultured oysters, are functioning, we developed a prey-predator model. Phytoplankton in different size categories were quantified, with a particular focus on phytoplankton smaller than 5 μm, which represent suitable food sources for oyster larvae during the planktonic phase. Filter feeding animals that compete with oysters were also identified and counted. Our numerical model consisted of 25 compartments, including inorganic/organic substances, phytoplankton, zooplankton, oysters, other filter feeding animals, and fish. The model outputs reproduced the observed temporal variation of the various parameters well, including the different size categories of oyster larvae from just spawning to settlement. Sensitivity analyses showed that an increase in the dissolved inorganic phosphorus load to 10 times than present value (0.2 mg P $m^{-3}$ $d^{-1}$) enhanced phytoplankton production, including that of small-sized phytoplankton, facilitating an increase of 51% in the successful settlement of oyster spat. In conclusion, the recent low success rates in the settlement of oyster larvae appear to be driven by insufficient quantities of the phytoplankton on which they feed. This lack of phytoplankton stems mainly from the reduction in the nutrient load in addition to competition between oysters and various other filter feeders for these food resources.

## 1. Introduction

Hiroshima Bay is the main area where oysters are produced in Japan, accounting for approximately 60% of Japan's total oyster production (Yamamoto et al., 2017). However, production in this area has decreased by ca. 24% over the last 13 years (Ministry of Internal Affairs and Communication Japan, 2014). In 2014, the successful collection of oyster larvae was extremely low, representing just 20% of the amount required by farmers (Hiroshima Fisheries and Promotion Center, 2017). In 2017, the collection of oyster larvae was again low, representing just 30% of that required. Around half the farmers are expected to abandon oyster farming if two successive years of collection prove unproductive.

One possible cause for the decrease in oyster production is declines in nutrient inflows. Yamamoto et al. (2002) and recently Kittiwanich et al. (2016) reported that Hiroshima Bay is under an oligotrophic condition, in which phosphorus (P) is the nutrient regulating phytoplankton growth in the bay. The decrease in P load since 1978 is because of the implementation of the Law of Concerning Special Measure for Conservation of the Environment of the Seto Inland Sea. In addition to P, nitrogen (N) has decreased since 1980. As a result of these measures, the transparency of the seawater in the bay has significantly recovered (Yamamoto and Wanishi, 2010). Thus, the decline in P and N load might have reduced the abundance of phytoplankton in Hiroshima Bay. In the present paper, we aim to ascertain whether P or N determines the decrease in phytoplankton production, and which is responsible for the decrease in oyster larvae.

Phytoplankton are the major food source for all filter feeders, including oysters (Ren and Schiel, 2008; Cugier et al., 2010). Because oyster larvae only feed on nano-sized phytoplankton of $<5$ μm diameter (Rico-Villa et al., 2009), it is necessary to ascertain whether the concentrations of such small-sized phytoplankton is sufficient for oyster larvae in Hiroshima Bay. This food source might be vital for the successful settlement of larvae.

Another concern regarding the settlement success of oyster larvae is

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https://doi.org/10.1016/j.aquaculture.2020.735564
Received 30 October 2019; Received in revised form 15 May 2020; Accepted 28 May 2020
Available online 05 June 2020

their ability to escape predation by adult filter feeders because oyster larvae are also planktonic organisms that form a nutritious food resource for other filter feeders. Even adult oysters may predate on oyster larvae, a behavior known as larviphagy (Troost et al., 2008). Although existing studies on larviphagy have been primarily performed in the laboratory, the filtration pressure of adult oysters is high in areas where oysters are cultured, which might contribute to the decline in the recruitment of oyster larvae.

Nutrient loads might not be sufficient for the growth of oysters in Hiroshima Bay (Kittiwanich et al., 2006), and this might be exacerbated by certain environmental conditions (Songsangjinda et al., 1999). However, the amount of nutrients needed for the recruitment of oyster larvae has not yet been quantified. If the nutrient enrichment can lead successful recruitment of oyster larvae, releasing more nutrients from rivers into the bay and/or local fertilization can be useful strategies to maintain oyster production. Thus, in the present study, we investigated which factors determine the successful recruitment of oyster larvae. Specifically, we explored bottom-up forces (i.e., nutrient load) versus top-down forces (i.e., predation), using a prey-predator numerical model. The outcomes of our study may provide a reference for local government, facilitating decisions on how to control the bay ecosystem to sustain oyster production.

## 2. Materials and methods

Hiroshima Bay is located in the western part of the Seto Inland Sea of Japan. The bay is separated into a northern and southern area. Most of the oyster culture rafts are situated in northern part of Hiroshima Bay (nHB). Fishermen culture oysters by hanging them under floating rafts that are 20 m × 10 m in length and width and extend to 15 m depth.

### 2.1. Field observations

Field observations were carried out at five stations located in nHB from June to August 2016 (Fig. 1). The study site covered a surface area of 160 $km^2$ with average water depth of 17.7 m. To analyze the environmental conditions in the bay, 50 ml of seawater was collected from the surface water at the five stations. Phytoplankton species were identified, and the number of cells was counted using an inverted microscope (Eclipse TS100, Nikon Corporation) for a 50 μl aliquot of the water sample. The phytoplankton community was divided into two size categories (small-sized <5 μm and large-sized phytoplankton larger than 5 μm) for observation and calculation (described later). Round-shaped single celled phytoplankton species that are smaller than 5 μm in size are supposed to be suitable food resources for oyster larvae (Rico-Villa et al., 2009). The chlorophyll *a* (Chl. *a*) concentration was determined for the water samples after size fractionation with a 5 μm pore size net and without fractionation (total) for 300 ml water samples using the method of SCOR/UNESCO (Strickland and Parsons, 1972). Temperature and underwater fluorescence were monitored at each station (Stn) during the study period (June–September 2016) using underwater fluorescent-turbid probes (Infinity CLW, JFE Advantech Co. Ltd.). Salinity data in the study area during the observation period were obtained from the monitoring report of the Hiroshima Fisheries Promotion Center.

To monitor the size and number of oyster larvae, water samples were collected by integrating from 0 to 5 m depth using a hose at the five stations during the oyster spawning season. Oyster larvae were subsequently counted under a microscope by the Hiroshima Fisheries Promotion Center. The Center personnel placed larvae into four groups depending on size: small (>90–150 μm), medium (150–210 μm), large (210–270 μm), and settling size (>300 μm).

To estimate the abundance of living organisms that might be classified as predators of phytoplankton in nHB, we collected samples from the surface water, oyster rafts and shoreline. In the surface water at five stations, zooplankton, along with larger-sized phytoplankton, were collected by vertically hauling a plankton net with a 72 μm mesh from 10 m depth to the surface to measure settling volume. The zooplankton samples were immediately preserved in 5% formalin in the final concentration and were transferred to the laboratory in Hiroshima University for counting and identification. Jellyfish were collected by vertically hauling a net with 1 cm mesh. Visual observations were conducted during the research cruises, and jellyfish density was roughly estimated by eye. In addition, attached organisms on rocks and concrete blocks at seven shoreline stations (SA) and at three oyster raft stations were observed (Fig. 1). At the shoreline stations, samples were collected from a 10 cm × 10 cm area using a quadrat in triplicate. At the oyster raft stations, whole oyster clusters were collected from 1 m and 4 m depths from one culture wire. The samples were kept in cool dark boxes and were transferred to the laboratory for identification, quantification, and weighing on the same day.

Several fish species might also contribute to prey-predator systems in nHB. Therefore, three GoPro cameras (Hero 4 video session) were placed on the raft at 5 m depth, separated by 2.5 m distances, to record fish for 1 h. Cameras were operated at three oyster rafts. Any fish that entered the field of view were identified, and the number of individuals per minute was counted. To estimate the density of mobile fish species, D (Ind. $m^{-3}$), and weight of fish, W (g $m^{-3}$), we used the length-weight relationship.

### 2.2. Model construction

To elucidate material cycles in nHB, we constructed a numerical model to express P and N flows in prey-predator interactions. The dominant organisms for which abundance was higher than 5% of the total number were incorporated in the model for oysters attached to oyster rafts and shoreline areas. As illustrated in Fig. 2, the model had 25 compartments: large-sized phytoplankton (PHY-L), small-sized phytoplankton (PHY-S), zooplankton (ZOO), oysters (OYS), oyster larvae small-size (OYSL-s), oyster larvae medium-size (OYSL-m), oyster larvae large-size (OYSL-l), oyster larvae settling-size (OYSL-st), mussels (MUS), mussels at the shoreline areas (MUS-sh), barnacles (BNC), barnacles at the shoreline areas (BNC-sh), polychaetes (POLY), clam worms (CWO), black seabream *Acanthopagrus schegelii* (BBS), puffer fish *Takifugu niphobles* (PFI), black scraper *Thammanocus modestus* (BSC), Japanese seabass *Lateolabrax japonius* (JSB), black rock fish *Sebastes inermis* (BRF), dissolved inorganic P (DIP), dissolved organic P (DOP), and detrital P (DET-P), dissolved inorganic N (DIN), dissolved organic N (DON), and detritus N (DET-N).

Considering that small-sized phytoplankton (<5 μm) are suitable food sources for oyster larvae (Rico-Villa et al., 2009), two phytoplankton compartments were included in the model based on size differences: large-sized phytoplankton (>5 μm) and small-sized phytoplankton (<5 μm). Four oyster larvae compartments were incorporated, based on the above mentioned datasets from microscopic investigation of the size and developmental stage prepared by Hiroshima City Fisheries Promotion Center: small size (>90–150 μm), medium size (150–210 μm), large size (210–270 μm), and settling size (270–300 μm).

The symbols with definitions and units used in the model are listed in Table 1. The mass balance equations for each compartment and the equations expressing the respective process are described in Tables 2 and 3, respectively.

The Ohta River is the major river flowing into nHB, providing ca.

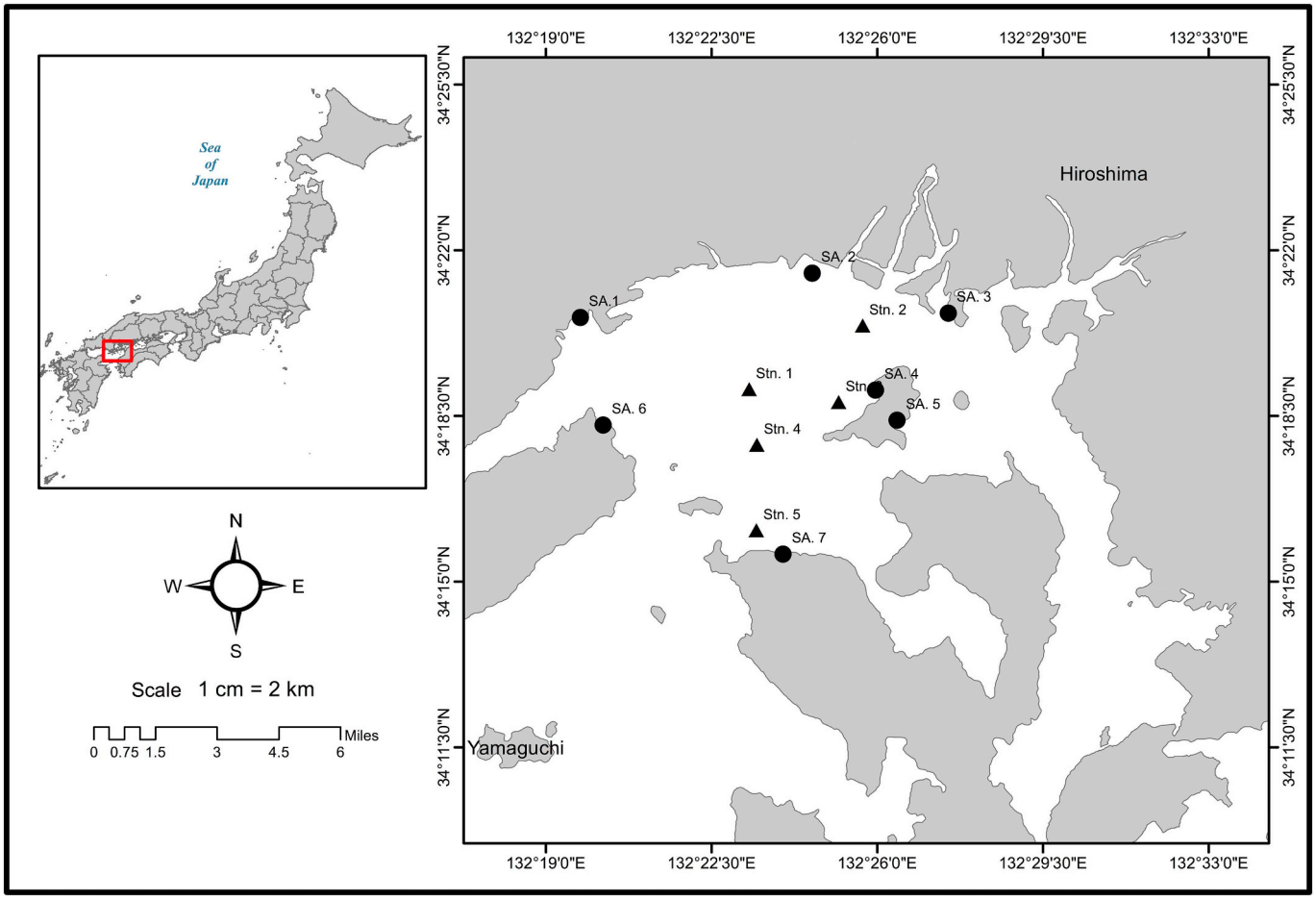


**Fig. 1.** Map showing the northern part of Hiroshima Bay, and the locations of the sampling stations. ▲, oyster raft stations (Stn); ●, shoreline stations (SA).

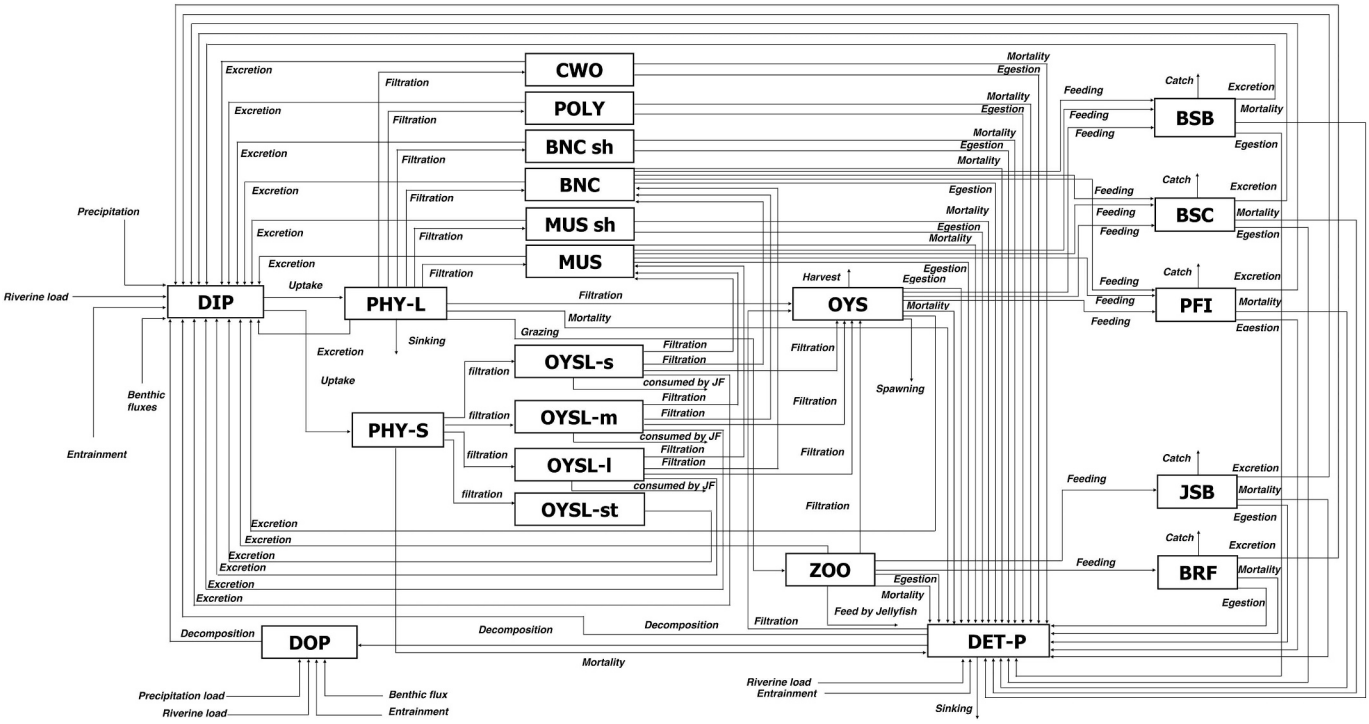


**Fig. 2.** Framework of phosphorus cycles in the northern part of Hiroshima Bay; stock (mg P $m^{-3}$) and fluxes (mg P $m^{-3}$ $d^{-1}$). Nitrogen cycles are omitted for simplicity.

**Table 1**
Summary of symbols, definitions, and units used in the model developed in this study.

| Symbol | Meaning | Unit |
|---|---|---|
| DIP | Dissolved inorganic phosphorus concentration in water column | mg P $m^{-3}$ |
| NH | Ammonium concentration in water column | mg N $m^{-3}$ |
| NO | Nitrate concentration in water column | mg N $m^{-3}$ |
| DOP, DON | Dissolved organic phosphorus or nitrogen concentration | mg P or N $m^{-3}$ |
| DET-P, DET-N | Detrital phosphorus or nitrogen concentration | mg P or N $m^{-3}$ |
| PHY-L, PHY-S | Phytoplankton biomass (L: large size, S: small size) | mg P $m^{-3}$ |
| ZOO | Zooplankton biomass | mg P $m^{-3}$ |
| *OYS* | Oyster biomass | mg P $m^{-3}$ |
| *OYSL-s, −m, −l, −st* | Oyster larvae biomass; small, medium, large and settling size | mg P $m^{-3}$ |
| *MUS, MUSsh* | Mussel biomass at oyster rafts and shoreline area | mg P $m^{-3}$ |
| *BNC, BNCsh* | Barnacle biomass at oyster rafts and shoreline area | mg P $m^{-3}$ |
| *CWO* | Clam worm biomass | mg P $m^{-3}$ |
| *POLY* | Polychaeta biomass | mg P $m^{-3}$ |
| *BSB* | Black sea bream biomass | mg P $m^{-3}$ |
| *BSC* | Black scraper biomass | mg P $m^{-3}$ |
| *PFI* | Pufferfish biomass | mg P $m^{-3}$ |
| *JSB* | Japanese sea bass biomass | mg P $m^{-3}$ |
| *BRF* | Black rock fish biomass | mg P $m^{-3}$ |
| $Riverine_{load}$ | Phosphorus and nitrogen loads through the Ohta River | mg P or N $m^{-3}$ $d^{-1}$ |
| *Entrainment* | Phosphorus and nitrogen loads from sHB by entrainment (estuarine circulation) | mg P or N$m^{-3}$ $d^{-1}$ |
| *Benthic flux* | Phosphorus load from the bottom sediments | mg P or N $m^{-3}$ $d^{-1}$ |
| $sHB_{in}$ | Phosphorus and nitrogen inputs by tidal exchange from southern Hiroshima Bay | mg P or N $m^{-3}$ $d^{-1}$ |
| *N* | Number of individuals | Ind. $m^{-3}$ |
| *Mort* | Mortality | mg P $m^{-3}$ $d^{-1}$ |
| *EXC* | Excretion | mg P $m^{-3}$ $d^{-1}$ |
| *EGEST* | Egestion | mg P $m^{-3}$ $d^{-1}$ |
| $Grazing_{zoo}$ | Grazing phytoplankton by zooplankton | mg P $m^{-3}$ $d^{-1}$ |
| $Consumed_{JF}$ | Oyster larvae consumed by jellyfish | mg P $m^{-3}$ $d^{-1}$ |
| *Filt* | Filtration by filter feeder | mg P $m^{-3}$ $d^{-1}$ |
| *Feeding* | Feeding by fish | mg P $m^{-3}$ $d^{-1}$ |
| *Catch* | Fish catch | mg P $m^{-3}$ $d^{-1}$ |
| $Decom_{DETP1}$ | Decomposition of DET-P to DIP | mg P $m^{-3}$ $d^{-1}$ |
| $Decom_{DETP2}$ | Decomposition of DET-P to DOP | mg P $m^{-3}$ $d^{-1}$ |
| $Decom_{DOP}$ | Decomposition of DOP to DIP | mg P $m^{-3}$ $d^{-1}$ |
| $Decom_{DETN1}$ | Decomposition of DET-N to NH | mg N $m^{-3}$ $d^{-1}$ |
| $Decom_{DETN2}$ | Decomposition of DET-N to DON | mg N $m^{-3}$ $d^{-1}$ |
| $Decom_{DON}$ | Decomposition of DON to NH | mg N $m^{-3}$ $d^{-1}$ |
| *Nitri* | Nitrification | mg N $m^{-3}$ $d^{-1}$ |
| *Denitri* | Denitrification | mg N $m^{-3}$ $d^{-1}$ |
| *D* | Fish density | Ind. $m^{-3}$ |
| *Ni* | Number of fishes seen in a scene | Ind. |
| *r* | Area observed | $m^{-3}$ |
| *W* | Fish weight | g |
| *L* | Fish length | cm |

90% of the total freshwater input, while the rest comes from the Seno River and the Yahata River (Yamamoto et al., 1998). The reported average concentrations of DIP and total P (TP) in the Ohta River water were 0.061 [1] and 0.10 mg $l^{-1}$, respectively (Yamamoto et al., 2002). The average concentration of ammonium (NH), nitrate (NO), and total N (TN) was 0.02, 0.40, and 0.58 mg $l^{-1}$, respectively (Japan River Association, 2016). These values were multiplied by river water discharge ranging from 24 to 4000 $m^3$ $s^{-1}$ (Japan's Rivers Association; www1.river.go.jp) to obtain riverine DIP, TP, DIN, and TN loads. The benthic fluxes of DIP, DOP, DIN, and DON from the sediment to the water column were obtained from Yamamoto et al. (1998), and we calculated their diffusion fluxes to the surface 10 m depth using the reported exchange rate between the upper layer and lower layer (Kittiwanich et al., 2016). The average seawater exchange rate during summer at the bay mouth, 0.2 per day, was applied according to Yamamoto et al. (2002).

The rate of growth of phytoplankton depends on nutrients, water temperature, and light intensity in the bay. We used the equations of Steele (1962) for phytoplankton response to light intensity, Blackman's law for minimum DIP limitation, and Eppley (1972) for the temperature of maximum photosynthetic rate. Phytoplankton biomass varies depending on growth, grazing by zooplankton, filter feeding by oysters, mussels, and barnacles, sinking, and mortality (Table 2). We used 0.01 mg $P^{-1}$ $m^{-3}$ $d^{-1}$ (Kawamiya et al., 1995) and 0.05 m $day^{-1}$ (Yanagi and Onitsuka, 2000) as the coefficient of mortality and sinking of phytoplankton, respectively (Table 4).

Oyster abundance in nHB was estimated using the following method. The total number of individual oysters was estimated as 320,332,800 by multiplying the average number of individuals in one cluster (15 Ind.) with the number of clusters in one line (40) and the number of lines used in one raft (688 lines per raft), and total number of oyster rafts (776 rafts) cultured in the summer season in the nHB.

To estimate the P content in all animals, we used the percentage (%) of P of animal biomass obtained from published papers. The P content in OYS tissue (meat) was 169 mg P per 100 g of oyster meat (Aquaculture New Zealand, 2017). We used 0.1% ash fresh dry weight (AFDW) of mussels to estimate the P content (Winter, 1973). According to Geraci et al. (2008), the P content in barnacle meat is 9.4 mg P per 1.037 Ind. These values were multiplied by the biomass of barnacles in nHB (avg. 0.48 Ind. $m^{-3}$). We used 0.14% P content in the total weight of POLY and CWO, based on Nielsen et al. (1995). For P content in fishes, we used 0.9% to 1.1% of 100 g fish meat (Ghaddar and Saoud, 2012).

We modified the equation for the filtration rate of oysters from Raillard et al. (1993) and Ehrich and Harris (2015), where the filtration rate was calculated as a function of individual dry weight, temperature, and salinity (Table 3). The dry weight of individual oysters was estimated from the measured wet weight using the equation reported by Kobayashi et al. (1997). The loss of spawning during summer was estimated using the equation proposed by Kawaguchi et al. (2011). P removal through harvesting by fishermen was estimated using the P content of oyster meat multiplied by the reported harvested amount. A filtration rate of 26 ml $h^{-1}$ was used for mussels, which was reported for mussels with shell lengths of 12 mm (Winter, 1973). A pumping rate of 2.0 to 8.8 ml $h^{-1}$ was used for barnacles following Hughes et al. (2005). We used the shell length correlation to estimate the filtration rate of oyster larvae (Gerdes, 1983). We used 120–250 μm shell length for oyster larvae.

Adult oysters filter a combination of phytoplankton, detritus, oyster larvae, and zooplankton nauplii. Oyster larvae are filtered at a rate that is 50% less than that of algae (Troost et al., 2009). The process of adult oysters consuming zooplankton nauplii was also incorporated in the model using the filtration rate of oysters and the ratio of consumption following Troost et al. (2008). The authors reported that the stomach contents of adult *Crassostrea gigas* collected from the Oosterschelde Estuary (Netherlands) included numerous zooplanktons. Zooplankton grazing on phytoplankton was expressed using Ivlev (1961).

We checked whether P or N governs the Hiroshima Bay ecosystem prior to running the model. We used two methods to identify which

**Table 2**
Mass balance equations used in the model.

| | | |
|---|---|---|
| $\frac{dDIP}{dt}$ | = | $DIP + Decom_{DOP} + Decom_{DETP1} + EXC_{load} + Riverine_{load} + Precipitation + Entrainment + Benthicflux + EXC_{PHYL} + EXC_{PHYS} + EXC_{ZOO} + EXC_{OYS} + EXC_{OYSLs} + EXC_{OYSLm} + EXC_{OYSLl} + EXC_{OYSLst} + EXC_{MUS} + EXC_{MUSsh} + EXC_{BNC} + EXC_{BNCsh} + EXC_{POLY} + EXC_{CWO} + EXC_{BSB} + EXC_{BSC} + EXC_{PFI} + EXC_{JSB} + EXC_{BRF} - Growth_{PHYL} - Growth_{PHYS}$ |
| $\frac{dNH}{dt}$ | = | $NH + Riverine_{load} + Precipitation + Entrainment + Benthic\ flux + Decom_{DETN1} + Decom_{DON} - Growth_{PHYL} - Growth_{PHYS} - Nitrification$ |
| $\frac{dNO}{dt}$ | = | $NO + Riverine_{load} + Precipitation + Entrainment + Benthic\ flux - Growth_{PHYL} - Growth_{PHYS} - Denitrification$ |
| $\frac{dDOP}{dt}$ | = | $DOP + Riverine_{load} + Precipitation + Entrainment + Benthic\ flux + Decom_{DETP2} - Decom_{DOP}$ |
| $\frac{dDON}{dt}$ | = | $DOP + Riverine_{load} + Precipitation + Entrainment + Benthic\ flux + Decom_{DETN2} - Decom_{DON}$ |
| $\frac{dDETP}{dt}$ | = | $DETP + Riverine_{load} + Benthic\ flux + Entrainment + Mort_{PHYL} + Mort_{PHYS} + Mort_{ZOO} + Mort_{OYS} + Mort_{OYSLs} + Mort_{OYSLm} + Mort_{OYSLl} + Mort_{OYSLst} + Mort_{MUS} + Mort_{MUSsh} + Mort_{BNC} + Mort_{BNCsh} + Mort_{CWO} + Mort_{POLY} + Mort_{BSB} + Mort_{BSC} + Mort_{PFI} + Mort_{JSB} + Mort_{BRF} + Fae_{ZOO} + Fae_{OYS} + Egest_{OYSLs} + Egest_{OYSLm} + Egest_{OYSLl} + Egest_{OYSLst} + Egest + Egest_{MUSsh} + Egest_{BNC} + Egest_{NCsh} + Egest_{CWO} + Egest_{POLY} + Egest_{BSB} + Egest_{BSC} + Egest_{PFI} + Egest_{JSB} + Egest_{BRF} - Filt_{OYS3} - Sink_{DETP} - Decom_{DETP1} - Decom_{DETP2})$ |
| $\frac{dDETN}{dt}$ | = | $DETN + Riverine_{load} + Benthic\ flux + Entrainment + Mort_{PHYL} + Mort_{PHYS} + Mort_{ZOO} + Mort_{OYS} + Mort_{OYSLs} + Mort_{OYSLm} + Mort_{OYSLl} + Mort_{OYSLst} + Mort_{MUS} + Mort_{MUSsh} + Mort_{BNC} + Mort_{BNCsh} + Mort_{CWO} + Mort_{POLY} + Mort_{BSB} + Mort_{BSC} + Mort_{PFI} + Mort_{JSB} + Mort_{BRF} + Fae_{ZOO} + Fae_{OYS} + Egest_{OYSLs} + Egest_{OYSLm} + Egest_{OYSLl} + Egest_{OYSLst} + Egest + Egest_{MUSsh} + Egest_{BNC} + Egest_{NCsh} + Egest_{CWO} + Egest_{POLY} + Egest_{BSB} + Egest_{BSC} + Egest_{PFI} + Egest_{JSB} + Egest_{BRF} - Filt._{OYS} - Sink_{DETN} - Decom_{DETN1} - Decom_{DETN2}$ |
| $\frac{dPHYL}{dt}$ | = | $PHYL + Growth_{PHYL} - Sink_{PHYL} - Mort_{PHYL} - Grazing_{ZOO} - EXC_{PHYL} - Filt_{OYS1} - Filt_{MUS1} - Filt_{MUSsh} - Filt_{BNC1} - Filt_{BNCsh} - Filt_{CWO} - Filt_{POLY}$ |
| $\frac{dPHYS}{dt}$ | = | $PHYS + Growth_{PHYS} - Sink_{PHYS} - Mort_{PHYS} - Grazing_{ZOO} - EXC_{PHYL} - Filt_{OYSLs} - Filt_{OYSLm} - Filt_{OYSLl} - Filt_{OYSLst}$ |
| $\frac{dZOO}{dt}$ | = | $ZOO + Grazing_{ZOO} - Filt_{OYS2} - Mort_{ZOO} - EXC_{ZOO} - Fae_{ZOO} - Feeding_{JF} - Feeding_{JSB} - Feediing_{BRF}$ |
| $\frac{dOYS}{dt}$ | = | $OYS + Filt_{OYS1} + Filt_{OYS2} + Filt_{OYS3} + Filt_{OYS4} + Filt_{OYS5} + Filt_{OYS6} - Fae_{OYS} - EXC_{OYS} - Spawning_{OYS} - Harvest_{OYS} - Mort_{OYS} - Feeding_{BSB3} - Feeding_{BSC3} - Feeding_{PFI3}$ |
| $\frac{dOYSL_s}{dt}$ | = | $OYSL_s + Filt_{OYSLs} - EXC_{OYSLs} - Fae_{OYSLs} - Filt_{OYS4} - Filt_{MUS3} - Filt_{BNC3} - Consumed_{JF1}$ |
| $\frac{dOYSL_m}{dt}$ | = | $OYSL_m + Filt_{OYSLm} - EXC_{OYSLm} - Fae_{OYSLm} - Filt_{OYS5} - Filt_{MUS4} - Filt_{BNC4} - Consumed_{JF2}$ |
| $\frac{dOYSL_l}{dt}$ | = | $OYSL_l + Filt_{OYSLl} - EXC_{OYSLl} - Fae_{OYSLl} - Filt_{OYS6} - Filt_{MUS5} - Filt_{BNC5} - Consumed_{JF3}$ |
| $\frac{dOYSL_{st}}{dt}$ | = | $OYSL_{st} + Filt_{OYSLst} - EXC_{OYSLst} - Fae_{OYSLst}$ |
| $\frac{dMUS}{dt}$ | = | $MUS + Filt_{MUS1} + Filt_{MUS2} + Filt_{MUS3} + Filt_{MUS4} - EXC_{MUS} - EGEST_{MUS} - Mort_{MUS} - Feeding_{BSB1} - Feeding_{PFI1} - Feeding_{BSC1}$ |
| $\frac{dMUS_{sh}}{dt}$ | = | $MUSsh + Filt_{MUSsh} + EXC_{MUSsh} + EGEST_{MUSsh} + Mort_{MUSsh}$ |
| $\frac{dBNC}{dt}$ | = | $BNC + Filt_{BNC1} + Filt_{BNC2} + Filt_{BNC3} + Filt_{BNC4} - EXC_{BNC} - EGEST_{BNC} - Mort_{BNC} - Feeding_{BSB2} - Feeding_{PFI2} - Feeding_{BSC2}$ |
| $\frac{dBNC_{sh}}{dt}$ | = | $BNCsh + Filt_{BNCsh} - EXC_{BNCsh} - EGEST_{BNCsh} - Mort_{BNCsh}$ |
| $\frac{dCWO}{dt}$ | = | $CWO + Filt_{CWO} - EXC_{CWO} - EGEST_{CWO} - Mort_{CWO}$ |
| $\frac{dPOLY}{dt}$ | = | $POLY + Filt_{POLY} - EXC_{POLY} - EGEST_{POLY} - Mort_{POLY}$ |
| $\frac{dBSB}{dt}$ | = | $SBS + Feeding_{SBS1} + Feeding_{BSB2} + Feeding_{BSB3} - Mort_{BSB} - EXC_{BS} - Egest_{BSB} - Catch_{BSB}$ |
| $\frac{dBSC}{dt}$ | = | $BSC + Feeding_{BSC1} + Feeding_{BSC2} + Feeding_{BSC3} - Mort_{BSC} - EXC_{BSC} - Egest_{BSC} - Catch_{BSC}$ |
| $\frac{dPFI}{dt}$ | = | $PFI + Feeding_{PFI1} + Feeding_{PFI2} + Feeding_{PFI3} - Mort_{PFI} - EXC_{PFI} - Egest_{PFI} - Catch_{PFI}$ |
| $\frac{dJSB}{dt}$ | = | $JSB + Feeding_{JSB} - Mort_{JSB} - EXC_{JSB} - Egest_{JSB} - Catch_{JSB}$ |
| $\frac{dBRF}{dt}$ | = | $BRF + Feeding_{BRF} - Mort_{BRF} - EXC_{BRF} - Egest_{BRF} - Catch_{BRF}$ |

nutrient governed the system. The first method calculated the DIN/DIP ratio in sea water and compared it to the Redfield ratio (16), because phytoplankton mainly utilize these inorganic forms. If the ratio is high, the system is judged to have a shortage of P and, thus, be governed by P and vice versa. The second method calculated the uptake rate of DIN and DIP using the model and examined which element was limiting the phytoplankton growth by comparison with the Redfield ratio. Both results are shown below.

The model was developed using the software Stella Architect (version 1.4.3), which was run with a time step of 0.02 d by the fourth-order Runge-Kutta method. The model outputs were validated using the observation data of the current study.

Sensitivity analyses were conducted to determine which parameters contributed to higher and lower recruitment of oyster larvae. One plausible parameter was the DIP load through the river, because the environmental law to alleviate eutrophicated water quality was likely to have been very effective in reducing loads over the last 40 years. Thus, sensitivity analyses were conducted for DIP loads that were $\times 2$, $\times 5$, and $\times 10$ times higher than present conditions. This phenomenon might cause small-sized phytoplankton and oyster larvae biomass to increase. Another plausible parameter was feeding pressure from adult oysters because they are intensively cultured in the bay and are likely feed on their own larvae. To test this, the number of adult oysters was reduced in the model. A decrease in the number of adult oysters was expected to cause an increase in phytoplankton biomass, possibly relaxing larviphagy.

**Table 3**
Summary of equations used in the model.

| | | Equation expression | References |
|---|---|---|---|
| $Riverine_{loadDIP}$ | = | $River_{DIP}$ x $\frac{FD_{OR}}{V}$ | 1 |
| $DIP_{load}$ | = | 2.76 x $10^{-9}$ x ($freshwater\ discharge$ (x$10^7 m^3 day^{-1}$))$^{0.824}$ | 1 |
| $Precipt_{loadDIP}$ | = | $Precipt_{DIP}$ x Precipt | – |
| $Growth_{PHYL}$ | = | $\mu max$ xexp($K_T$ x $T$)x MIN $\left[\frac{NH_4^+ + NO_3^-}{NH_4^+ + NO_3^- + K_{SP}}, (DIP/(DIP + K_{SP}))\right]$ x $\frac{I}{I_{opt}}$ x exp$\left(1 - \left(\frac{I}{I_{opt}}\right)\right)$ x $PHYL$ | 2 |
| $Grazing_{ZOO}$ | = | $G_{max}$ x exp ($K_T$ x $T$)x [1 − $exp\ \lambda(PHYL^* - PHYL)$]x ZOO | 3 |
| $Filt_{OYS}$ | = | [2.51 x (0.225$ww$ − 0.193)$^{0.279}$ x 0.5943 xln(T) − 0.9958] x N x (PHYL + DETP + ZOO + $OYSL_s$ + $OYSL_m$ + $OYSL_l$) x (1 + $TAN(salinity - 7.5)$) | 4 |
| $Filt_{MUS}$ | = | $K_{filtMUS}$ x $N_{MUS}$ x (PHYL + $OYSL_s$ + $OYSL_m$ + $OYSL_l$) | – |
| $Filt_{BNC}$ | = | $K_{filtBNC}$ x $N_{BNC}$ x (PHYL + $OYSL_s$ + $OYSL_m$ + $OYSL_l$) | – |
| $Filt_{MUSsh}$ | = | $K_{filtMUSsh}$ x $N_{MUSsh}$ x PHYL | – |
| $Filt_{BNCsh}$ | = | $K_{filtBNCsh}$ x $N_{BNCsh}$ x PHYL | – |
| $Filt_{POLY}$ | = | $K_{filtPOLY}$ x $N_{POLY}$ x PHYL | – |
| $Filt_{CWO}$ | = | $K_{filtCWO}$ x $N_{CWO}$ x PHYL | – |
| $Consumed_{JF}$ | | $K_{consumedJF}$ x $N_{JF}$ x OYSL | – |
| $Feeding_{BSB}$ | = | $K_{feedBSB}$ x (MUS + BNC + OYS) | – |
| $Feeding_{BSC}$ | = | $K_{feedBSC}$ x (MUS + BNC + OYS) | – |
| $Feeding_{PFI}$ | = | $K_{feedPFI}$ x (MUS + BNC + OYS) | – |
| $Feeding_{JSB}$ | = | $K_{feedJSB}$ x ZOO | – |
| $Feeding_{BRF}$ | = | $K_{feedBRF}$ x ZOO | – |
| $EXC_{PHYL}$ | = | $K_{excPHYL}$ x $growth_{PHYL}$ | 5 |
| $EXC_{ZOO}$ | = | $\alpha_{ZOO}$ x $grazing_{ZOO}$ x $ZOO$ | 5 |
| $EXC_{OYSadult}$ | = | $\alpha_{OYSadult}$ x $filt_{OYSadult}$ | 5 |
| $EXC_{MUS}$ | = | $\alpha_{MUS}$ x $filt_{MUS}$ | – |
| $EXC_{BNC}$ | = | $\alpha_{BNC}$ x $filt_{BNC}$ | – |
| $EXC_{MUSsh}$ | = | $\alpha_{MUSsh}$ x $filt_{MUSsh}$ | – |
| $EXC_{BNCsh}$ | = | $\alpha_{BNCsh}$ x $filt_{BNCsh}$ | – |
| $EXC_{CWO}$ | = | $\alpha_{CWO}$ x $filt_{CWO}$ | – |
| $EXC_{POLY}$ | = | $\alpha_{POLY}$ x $filt_{POLY}$ | – |
| $EXC_{BSB}$ | = | $\alpha_{BSB}$ x $feeding_{BSB}$ | – |
| $EXC_{BSC}$ | = | $\alpha_{BSC}$ x $feeding_{BSC}$ | – |
| $EXC_{PFI}$ | = | $\alpha_{PFI}$ x $feeding_{PFI}$ | – |
| $EXC_{JSB}$ | = | $\alpha_{JSB}$ x $feeding_{JSB}$ | – |
| $EXC_{BRF}$ | = | $\alpha_{BRF}$ x $feeding_{BRF}$ | – |
| $sink_{PHYL}$ | = | $K_{sinkPHYL}$ x PHYL x $\left(\frac{AV}{V}\right)$ | 5 |
| $sink_{DETP}$ | = | $K_{sinkDETP}$ x DETP x $\left(\frac{AV}{V}\right)$ | 5 |
| $sink_{DETN}$ | = | $K_{sinkDETN}$ x DETN x $\left(\frac{AV}{V}\right)$ | 5 |
| $fae_{ZOO}$ | = | $\beta_{ZOO}$ x $grazing_{ZOO}$ x $ZOO$ | 5 |
| $fae_{OYS}$ | = | $\beta_{OYS}$ x $filt_{OYS}$ | 5 |
| $Egest_{MUS}$ | = | $K_{MUS}$ x $filt_{MUS}$ | – |
| $Egest_{BNC}$ | = | $K_{BNC}$ x $filt_{BNCN}$ | – |
| $Egest_{MUSsh}$ | = | $K_{MUSsh}$ x $filt_{MUSsh}$ | – |
| $Egest_{BNCsh}$ | = | $K_{BNCsh}$ x $filt_{BNCsh}$ | – |
| $Egest_{CWO}$ | = | $K_{CWO}$ x $filt_{CWO}$ | – |
| $Egest_{POLY}$ | = | $K_{POLY}$ x $filt_{POLU}$ | – |
| $egest_{BSB}$ | = | $K_{BSB}$ x $feeding_{BSB}$ | – |
| $egest_{BSC}$ | = | $K_{TSF}$ x $feeding_{BSC}$ | – |
| $egest_{PFI}$ | = | $K_{PFI}$ x $feeding_{PFI}$ | – |
| $egest_{JSB}$ | = | $K_{JSB}$ x $feeding_{JSB}$ | – |
| $egest_{BRF}$ | = | $K_{BRF}$ x $feeding_{BRF}$ | – |
| $mort_{PHYL}$ | = | $K_{mortPHYL}$ xexp($k_T$ x $T$)x $PHYL^2$ | 5 |
| $mort_{ZOO}$ | = | $K_{mortZOO}$ xexp($k_T$ x $T$)x $ZOO^2$ | 5 |
| $mort_{OYS}$ | = | $K_{mortOYS}$ x $OYS$ | 5 |
| $mort_{MUS}$ | = | $K_{mortMUS}$ x $MUS$ | – |
| $mort_{BNC}$ | = | $K_{mortBNC}$ x $BNC$ | – |
| $mort_{MUSsh}$ | = | $K_{mortMUSsh}$ x $MUS_{sh}$ | – |
| $mort_{BNCsh}$ | = | $K_{mortBNCsh}$ x $BNC_{sh}$ | – |
| $mort_{CWO}$ | = | $K_{CWO}$ x $CWO$ | – |
| $mort_{POLY}$ | = | $K_{mortPOLY}$ x $POLY$ | – |
| $mort_{BSB}$ | = | $K_{mortBSB}$ x $BSB$ | – |
| $mort_{BSC}$ | = | $K_{mortBSC}$ x $BSC$ | – |
| $mort_{PFI}$ | = | $K_{mortPFI}$ x $PFI$ | – |
| $mort_{JSB}$ | = | $K_{mortJSB}$ x $JSB$ | – |
| $mort_{BRF}$ | = | $K_{mortBRF}$ x $BRF$ | – |
| $spaw_{OYS}$ | = | $10^{3.9ww}$x ($T$ − 10)$^2$ x $OYS$ | 6 |

(*continued on next page*)

**Table 3** (*continued*)

| | | Equation expression | References |
|---|---|---|---|
| $harv_{OYS}$ | = | $(0.225ww - 0.193)$ x $N_{harv}$ x$\frac{0.02}{v}$ | 7 |
| $catch_{BSB}$ | = | $K_{catchBSB}$ x $BSB$ | – |
| $catch_{BSC}$ | = | $K_{catcBSC}$ x $BSC$ | – |
| $catch_{PFI}$ | = | $K_{catchPFI}$ x $PFI$ | – |
| $catch_{JSB}$ | = | $K_{catchJSB}$ x $JSB$ | – |
| $catch_{BRF}$ | = | $K_{catchBRF}$ x $BRF$ | – |
| $decom_{DOP}$ | = | $K_{decomDOP}$ x exp ($k_T$ x $T$) $x$ $DOP$ | 6 |
| $decom_{DETP1}$ | = | $K_{decomDETP1}$ x exp ($k_T$ x $T$) $x$ $DETP$ | 6 |
| $decom_{DETP2}$ | = | $K_{decomDETP2}$ x exp ($k_T$ x $T$) $x$ $DETP$ | 6 |
| $decom_{DETN1}$ | = | $K_{decomDETN1}$ x exp ($k_T$ x $T$) $x$ $DETN$ | 6 |
| $decom_{DETN2}$ | = | $K_{decomDETN2}$ x exp ($k_T$ x $T$) $x$ $DETN$ | 6 |
| $Nitri$ | = | $K_{Nitri}$ x exp ($k_T$ x $T$) $x$ $NH$ | 6 |
| $Denitri$ | = | $K_{Denitri}$ x exp ($k_T$ x $T$)$x$ $(1 - DO)/(DO + K_{Onitri}) * NO$ | 6 |
| $D$ | = | $\frac{\sum_{i=1}^{p} Ni}{r}$ | 8 |
| $W$ | = | $aL^b$ | 8 |

*Sources:* 1. Yamamoto et al. (2002), 2. Modified from Steele (1962), Blackman (1905) , and Eppley (1972), 3. Ivlev (1961), 4. Modified from Raillard et al. (1993) and Ehrich and Harris (2015), 5. Kobayashi et al. (1997), 6. Kittiwanich et al. (2006), 7. Kawaguchi et al. (2011), 8. Yoon and Choi (2010).

## 3. Results

### 3.1. Environmental conditions

Temperature during the observation period ranged between 22 and 30 °C (Fig. 3a). The chl. *a* concentration was high at Stn. 1 near the Ohta River mouth during the first half (end of July) of the observation period, and became high at Stn. 3 in the southern part and Stn. 5 in the western part of the bay during the latter half of the observation period (Fig. 3a). Salinity, particularly in the surface layer, decreased at the beginning of July (Fig. 3b).

Among the phytoplankton species identified, *Skeletonema costatum, Nitzschia* sp., *Chaetoceros* sp., and *Leptocylindrus* sp. were dominant. Out of these four species, *Leptocylindrus* sp. was the most abundant (avg. $11.37 \times 10^3$ cells $ml^{-1}$), followed by *Chaetoceros* sp. (avg $7.87 \times 10^3$ cells $ml^{-1}$). However, the abundance of small-sized phytoplankton (<5 μm) was extremely low at all stations during the observation period, with values of $0.21 \times 10^3$ cell $ml^{-1}$ in July and $2.89 \times 10^3$ cell $ml^{-1}$ in August (Fig. 3d). The average across the entire observation period was $1.97 \times 10^3$ cells $ml^{-1}$.

The density of oyster larvae decreased from OYSL-s (8,949 Ind. $m^{-3}$) to OYSL-st (6.9 Ind. $m^{-3}$). A particularly large decline was observed from OYSL-s to OYSL-m (avg. 219 Ind. $m^{-3}$), as shown in Fig. 3e. Fig. 3e shows that the highest recruitment success of OYSL-st was 30 Ind. $m^{-3}$ at the end of August. This means only 0.16% of spawned larvae (ca. 9000 Ind. $m^{-3}$) survived and successfully settled.

### 3.2. Attached animals

Among the animals attached to oyster rafts, oysters were noticeably heavier (67.2 ± 2.2 g) than mussels (0.4 ± 0.2 g) and barnacles (3.4 ± 1.7 g) in weight but were less abundant than these other two groups in number (Fig. 4). The average size of oysters, mussels, and barnacles was 84, 12 and 22 mm, respectively, during the observation period from June to August. Although sea squirts and unidentified white shells were also found as attached organisms on oyster rafts, they were not considered in the model calculation, due to their small contributions in both number and weight. The animals observed along the shoreline were similar to those observed on the oyster rafts, in terms of species; however, barnacles had the highest abundance at all shoreline stations, where most were attached to concrete walls.

### 3.3. Model outputs

As shown in Fig. 5a, it was confirmed that P was the limiting factor of phytoplankton growth in nHB from both the DIN/DIP molar ratio of the water (Fig. 5a) and comparison of DIN and DIP uptake rate by phytoplankton (Fig. 5b). In Fig. 5a, only one date, 23 August, was shown to have an N limitation with a DIN/DIP molar ratio ~ 12. In regard to the uptake rate of DIN and DIP, it was judged that DIP was basically the limiting factor throughout the period with two exceptions in mid-June and around 20 August. The latter may be the same event as that observed in the DIN/DIP molar ratio. Based on these results, description below will be focused mainly on P cycles with reference to N cycles where relevant.

The estimated values for the various forms of N and P, except DIP, corresponded well with the observed values (Figs. 6a-f). Calculated PHY-L concentrations in the model were in the same range as the observed values, but with less fluctuation. PHY-S output showed very low levels with no significant temporal change, which was consistent with the observed values which were less than the detection limit (<0.5 mg P $m^{-3}$) throughout the period (Fig. 6g). It is likely that the scarcity of the small-sized phytoplankton affected the numbers of oyster larvae.

Oysters had the highest biomass of all observed filter feeding animals, both attached to the oyster rafts and along the shoreline of the bay. The average of OYS biomass was 2.85 mg P $m^{-3}$ during the observation period. The output levels of OYSL-s, OYSL-m, OYSL-l, and OYSL-st biomass of the model were in the same range as the observed values, but with less fluctuation (Figs. 6j-m). The calculated average values of OYSL-s, OYSL-m, OYSL-l, and OYSL-st biomass were 0.0046, 0.0003, 0.0003, and 0.0001 mg P $m^{-3}$ during the observation period, respectively.

### 3.4. Phosphorus cycles during the observation period

The average DIP concentration during the observation period (June to September) in nHB was 3.12 mg P $m^{-3}$ (Fig. 7). The average DIP load of the river during the observation period was estimated to be

**Table 4**
List of parameters used in the model.

| Symbol | Meaning | Unit | Value | References |
|---|---|---|---|---|
| $V$ | Water volume in northern part of Hiroshima Bay | $m^3$ | $22 \times 10^8$ | Yamamoto and Hatta (2004) |
| $AV$ | Surface area between upper and lower layers | $m^2$ | $160 \times 10^6$ | Kittiwanich et al. (2006) |
| $FD_{OR}$ | Freshwater Discharge of the Ohta River | $m^3\ d^{-1}$ | $24–40 \times 10^8$ | Japan River Association (2016) |
| $Precip$ | Precipitation | $mm\ d^{-1}$ | 0–79.5 | Japan Meteorological Agency (2016) |
| $I$ | Light intensity | $\mu mol\ m^{-2}\ d^{-1}$ | $19.7 \times 10^7$ | National Astronomical Observatory of Japan (2013) |
| $I_{opt}$ | Optimum light intensity | $\mu E\ m^{-2}\ d^{-1}$ | $2.93 \times 10^7$ | Kawamiya et al. (1995) |
| $T$ | Water temperature | °C | 24–30 | Observed |
| $K_T$ | Temperature coefficient | $°C^{-1}$ | 0.0693 | Eppley (1972) |
| $Chl\text{-}a$ | Chl *a* concentration | $\mu g\ l^{-1}$ | 1.2–11.3 | Observed |
| $\mu_{max}$ | Maximum specific growth rate of phytoplankton | $d^{-1}$ | 1.78 | Eppley (1972) |
| $K_{sP}$ | Half saturation constant for inorganic phosphorus uptake | $d^{-1}$ | 17 | Yanagi and Onitsuka (2000) |
| $K_{sN}$ | Half saturation constant for inorganic nitrogen uptake | $d^{-1}$ | 28 | Eppley (1972) |
| $K_{sinkPHY}$ | Sinking velocity of phytoplankton | $m\ d^{-1}$ | 0.5 | Hayashi and Yanagi (2002) |
| $G_{max}$ | Maximum grazing rate by zooplankton | $d^{-1}$ | 0.1 | Kawamiya et al. (1995) |
| ⁑ | Ivlev' constant | $d^{-1}$ | 0.72 | Kawamiya et al. (1995) |
| $PHY^*$ | Threshold of phytoplankton density for grazing | $mg\ P\ m^{-3}$ | 0.0833 | Kawamiya et al. (1995) |
| $G_{ZOO}$ | Grazing rate of zooplankton | $d^{-1}$ | 0.1 | Kawamiya et al. (1995) |
| $G_{JF}$ | Grazing rate of jellyfish | $d^{-1}$ | 0.21 | Uye and Shimauchi (2005) |
| $Consumed_{JF}$ | Oyster larvae %-consumption rate by jellyfish | $d^{-1}$ | 0.7% | Purcell et al. (1991) |
| $K_{filtMUS}$ | Filtration rate of mussel | $ml\ h^{-1}$ | 26 | Winter (1973) |
| $K_{fillBAR}$ | Filtration rate of barnacle | $ml\ h^{-1}$ | 4 | Hughes et al. (2005) |
| $K_{fillCWO}$ | Filtration rate of clam worm | $l\ d^{-1}$ | 6 | Nielsen et al. (1995) |
| $K_{fillPOLY}$ | Filtration rate of polychaeta | $l\ d^{-1}$ | 6 | Nielsen et al. (1995) |
| $K_{feedBSB}$ | Feeding rate of black sea bream | $d^{-1}$ | 0.03 | Khan et al. (2008) |
| $K_{feedBSC}$ | Feeding rate of black scraper | $d^{-1}$ | 0.07 | Miyajima et al. (2011) |
| $K_{feedPFI}$ | Feeding rate of pufferfish | $d^{-1}$ | 0.016 | Takii et al. (1997) |
| $K_{feedJSB}$ | Feeding rate of Japanese sea bass | $d^{-1}$ | 0.0032 | Xu et al. (2012) |
| $K_{feedBRF}$ | Feeding rate of black rock fish | $d^{-1}$ | 0.09 | Kono and Nose (1971) |
| $\alpha_{ZOO}$ | Constant for zooplankton excretion | $d^{-1}$ | 0.4 | Kawamiya et al. (1995) |
| $\alpha_{OYS}$ | Constant for oyster excretion | $d^{-1}$ | 0.08 | Kobayashi et al. (1997) |
| $\alpha_{MUS}$ | Constant for mussel excretion | $d^{-1}$ | 0.02 | Jansen et al. (2012) |
| $\alpha_{BNCBNC}$ | Constant for barnacle excretion | $d^{-1}$ | 0.00072 | Southward (1955) |
| $\alpha_{CWO}$ | Constant for clam worm excretion | $d^{-1}$ | 0.1 | Tuning |
| $\alpha_{POLY}$ | Constant for polychaeta excretion | $d^{-1}$ | 0.12 | Honda and Kikuchi (2002) |
| $\alpha_{BSB}$ | Constant for black sea bream excretion | $d^{-1}$ | 0.003 | Harris et al. (1986) |
| $\alpha_{BSC}$ | Constant for black scraper excretion | $d^{-1}$ | 0.003 | Tuning |
| $\alpha_{PFI}$ | Constant for pufferfish excretion | $d^{-1}$ | 0.002 | Kikuchi et al. (1996) |
| $\alpha_{JSB}$ | Constant for Japanese sea bass excretion | $d^{-1}$ | 0.003 | Tuning |
| $\alpha_{BRF}$ | Constant for black rock fish excretion | $d^{-1}$ | 0.009 | Harris et al. (1986) |
| $K_{DecomDOP}$ | Decomposition coefficient of DOP to DIP | $d^{-1}$ | 0.02 | Kawamiya et al. (1995) |
| $K_{DecomDETP1}$ | Decomposition coefficient of DET-P to DOP | $d^{-1}$ | 0.02 | Kawamiya et al. (1995) |
| $K_{DecomDETP2}$ | Decomposition coefficient of DET-P to DIP | $d^{-1}$ | 0.02 | Kawamiya et al. (1995) |
| $K_{DecomDETN1}$ | Decomposition coefficient of DET-N to NH | $d^{-1}$ | 0.02 | Kawamiya et al. (1995)3 |
| $K_{DecomDETN2}$ | Decomposition coefficient of DET-N to DON | $d^{-1}$ | 0.01 | Kawamiya et al. (1995) |
| $K_{DecomDON}$ | Decomposition coefficient of DON to NH | $d^{-1}$ | 0.01 | Kawamiya et al. (1995) |
| $K_{Nitri}$ | Nitrification rate in water at 0 °C | $d^{-1}$ | 0.08 | Kawamiya et al. (1995) |
| $K_{onitri}$ | Half saturation constant of oxygen | $g\ O_2\ m^{-3}$ | 2.0 | Chapelle et al. (2000) |
| $K_{denitri}$ | Denitrification rate in water at 0 °C | $d^{-1}$ | 0.5 | Hayashi and Yanagi (2002) |
| $\beta_{ZOO}$ | Constant for fecal pellet production by zooplankton | $d^{-1}$ | 0.03 | Kawamiya et al. (1995) |
| $\beta_{OYS}$ | Constant for fecal pellet production by oyster | $d^{-1}$ | 0.35 | Kusuki (1977) |
| $Kegest_{MUS}$ | Egestion rate of mussel | $d^{-1}$ | 0.02 | Jansen et al. (2012) |
| $Kegest_{BNC}$ | Egestion rate of barnacle | $d^{-1}$ | 0.0072 | Southward (1955) |
| $Kegest_{CWO}$ | Egestion rate of clam worm | $d^{-1}$ | 0.1 | Tuning |
| $Kegest_{POLY}$ | Egestion ate of polychaeta | $d^{-1}$ | 0.15 | Palmer (2009) |
| $Kegest_{BSB}$ | Egestion rate of black seabream | $d^{-1}$ | 0.03 | Winber (1960) |
| $Kegest_{BSC}$ | Egestion rate of black scraper | $d^{-1}$ | 0.006 | Tuning |
| $Kegest_{PFI}$ | Egestion rate of pufferfish | $d^{-1}$ | 0.006 | Kikuchi et al. (1996) |
| $Kegest_{JSB}$ | Egestion rate of Japanese sea bass | $d^{-1}$ | 0.004 | Tuning |
| $Kegest_{BRF}$ | Egestion rate of black rock fish | $d^{-1}$ | 0.018 | Winber (1960) |
| $Kmort_{PHY}$ | Mortality rate of phytoplankton | $mg\ P\ m^{-3}\ d^{-1}$ | 0.01 | Kawamiya et al. (1995) |
| $Kmort_{ZOO}$ | Mortality rate of zooplankton | $mg\ P\ m^{-3}\ d^{-1}$ | 0.0465 | Kawamiya et al. (1995) |
| $Kmort_{OYS}$ | Mortality rate of oyster | $d^{-1}$ | 0.1 | Gangnery et al. (2011) |
| $Kmort_{MUS}$ | Mortality rate of mussel | $d^{-1}$ | 0.04 | Mallet et al. (2008) |
| $Kmort_{BNC}$ | Mortality rate of barnacle | $d^{-1}$ | 0.0145 | Jenkins et al. (2008) |
| $Kmort_{CWO}$ | Mortality rate of clam worm | $d^{-1}$ | 0.04 | Qian and Chia (1994) |
| $Kmort_{POLY}$ | Mortality rate of polychaeta | $d^{-1}$ | 0.033 | Maurer et al. (1982) |
| $Kmort_{BSB}$ | Mortality rate of black seabream | $d^{-1}$ | 0.01 | Xiao et al. (2013) |
| $Kmort_{BSC}$ | Mortality rate of black scraper | $d^{-1}$ | 0.05 | Tuning |

(*continued on next page*)

**Table 4** (*continued*)

| Symbol | Meaning | Unit | Value | References |
|---|---|---|---|---|
| $Kmort_{PFI}$ | Mortality rate of pufferfish | $d^{-1}$ | 0.02 | Kato et al. (2005) |
| $Kmort_{JSB}$ | Mortality rate of Japanese sea bass | $d^{-1}$ | 0.07 | Shoji and Tanaka (2007) |
| $Kmort_{BRF}$ | Mortality rate of black rock fish | $d^{-1}$ | 0.01 | Wallace et al. (2008) |
| $Kcatch_{BSB}$ | Catch rate of black seabream | $d^{-1}$ | 0.2 | Yamamoto and Miyata (2018) |
| $Kcatch_{BSC}$ | Catch rate of black scraper | $d^{-1}$ | 0.2 | Tuning |
| $Kcatch_{PFI}$ | Catch rate of pufferfish | $d^{-1}$ | 0.1 | Öndes et al. (2018) |
| $Kcacth_{JSB}$ | Catch rate of Japanese sea bass | $d^{-1}$ | 0.054 | Tuning |
| $Kcacth_{BRF}$ | Catch rate of black rock fish | $d^{-1}$ | 0.05 | Yamamoto and Miyata (2018) |
| $L_{BSB}$ | length of BSB | cm | 28 | Observed |
| $L_{BSC}$ | length of BSC | cm | 12 | Observed |
| $L_{PFI}$ | length of PFI | cm | 15 | Observed |
| $L_{JSB}$ | length of JSB | cm | 40 | Observed |
| $L_{BRF}$ | length of BRF | cm | 15 | Observed |
| $a_{BSB}$ | Intercept for length-weight relationship of BSB | – | 0.04 | Chu et al. (2011) |
| $a_{BSC}$ | Intercept for length-weight relationship of BSC | – | 0.0218 | Mancera-Rodriguez and Castro-Hernandez (2015) |
| $a_{PFI}$ | Intercept for length-weight relationship of PFI | – | 0.05545 | Yoon and Choi (2010) |
| $a_{JSB}$ | Intercept for length-weight relationship of JSB | – | 0.0682 | Yoon and Choi (2010) |
| $a_{BRF}$ | Intercept for length-weight relationship of BRF | – | 0.05326 | Yoon and Choi (2010) |
| $b_{BSB}$ | Slope for the length-weight relationship of BSB | – | 2.95 | Chu et al. (2011) |
| $b_{BSC}$ | Slope for the length-weight relationship of BSC | – | 2.93 | Mancera-Rodriguez and Castro-Hernandez (2015) |
| $b_{PFI}$ | Slope for the length-weight relationship of PFI | – | 3.151 | Yoon and Choi (2010) |
| $b_{JSB}$ | Slope for the length-weight relationship of JSB | – | 2.491 | Yoon and Choi (2010) |
| $b_{BRF}$ | Slope for the length-weight relationship of BRF | – | 2.502 | Yoon and Choi (2010) |

0.20 mg P $m^{-3}$ $d^{-1}$. The freshwater discharge from the Ohta River peaked at 183 $m^3$ $s^{-1}$ for the daily average in July, which was almost four times higher than the 10-year average for 2006 to 2015 (49.3 $m^{-3}$ $s^{-1}$).

PHY-L was strongly filtered by OYS (0.86 mg P $m^{-3}$ $d^{-1}$), which was almost twice the amount filtered by ZOO (0.41 mg P $m^{-3}$ $d^{-1}$). Mussels were third in terms of PHY-L filtration, which was 1/20 of ZOO (0.02 mg P $m^{-3}$ $d^{-1}$; Fig. 6), followed by worms (0.0015 mg P $m^{-3}$ $d^{-1}$) and barnacles (0.0007 mg P $m^{-3}$ $d^{-1}$). On the other hand, ZOO was grazed at 0.12 and 0.05 mg P $m^{-3}$ $d^{-1}$ by OYS and jelly fish, respectively.

In comparison, PHY-S was specifically filtrated by OYSL. OYSL-s filtered PHY-S (0.0033 mg P $m^{-3}$) more strongly than oyster larvae of the other sizes (0.001–0.0002 mg P $m^{-3}$) during the observation period. OYSL was fed on by adult oysters, mussels, and barnacles at rates of 0.0006, <0.0003, and < 0.0003 mg P $m^{-3}$, respectively. The contribution of jelly fish to decrease oyster larvae biomass was also small (<0.0001 mg P $m^{-3}$ $d^{-1}$). Spawning by oysters was large being 0.66 mg P $m^{-3}$ in this season.

Predation from fish species with hard teeth, namely, BBS, PFI and BSC, on juvenile oysters was estimated to be 0.36, 0.24, 0.12 mg P $m^{-3}$. Fish catch was estimated to be 0.16 and 0.06 mg P $m^{-3}$ for JSB and BRS, respectively, which fed mainly on zooplankton.

### 3.5. Sensitivity analysis results

The increase in the nutrient load caused an increase in phytoplankton biomass. PHY-L biomass noticeably increased from an average of 4.15 mg P $m^{-3}$ (present value in 2016) to 14.8 mg P $m^{-3}$ with a × 10 increase in DIP load (Fig. 8). PHY-S, which are suitable food for oyster larvae, also noticeably increased with increasing DIP load. With a × 2 increase in DIP load, PHY-S increased from 0.23 mg P $m^{-3}$ under present conditions to 0.75 mg P $m^{-3}$, while a × 10 increase caused an increase of 1.15 mg P $m^{-3}$. The percentage increase in OYSL-st biomass was 38% and 53% with ×5 and ×10 increase in DIP load, respectively.

A × 5 increase in NH and NO loads caused a 17% increase in PHY-S biomass (Table 5). A × 10 increase caused a 21% increase in OYSL-st biomass. However, these increments were not as large as the increases from a greater DIP load.

In comparison, reducing the adult oyster biomass caused both phytoplankton and oyster larvae to increase (Fig. 9). The ×1/5 and ×1/10 reduction in OYS biomass caused OYSL-st biomass to increase by 13% and 20%, respectively. Thus, larviphagy contributes towards reducing the probability of oyster larvae recruitment, although this has a lower effect than the increase in DIP load. The effect of filtration by the other adult filter feeders (MUS and BNC) on oyster larvae was as low as that by adult oysters (<0.0001 mg P $m^{-3}$ $d^{-1}$).

## 4. Discussion

### 4.1. Bottom-up processes

Phytoplankton abundance drives the growth of oysters. Thus, reducing the phytoplankton concentration in the water column can have a large effect on the productivity of oysters. Yamamoto et al. (2002) and Kittiwanich et al. (2016) reported that P regulated phytoplankton biomass in Hiroshima Bay during the 1980s–1990s. However, the average DIP load observed during this study (440 kg P $d^{-1}$) was much lower than that (1.3 tons P $d^{-1}$) during the 1980s–1990s because the legislated measures to reduce P loads have been in force for around 40 years. When the legislation was revised in 2015, it was not considered that this measure would impact the productivity of coastal areas by limiting phytoplankton growth and, hence, oyster growth.

Nutrient loading from the river has dramatically decreased since the implementation of the Law of Concerning Special Measure for Conservation of the Environment of the Seto Inland Sea, which included Hiroshima Bay. According to Yamamoto et al. (2002), the TP load to the entire Seto Inland Sea decreased from ~80 tons P $d^{-1}$ to nearly the half that in 2000. Therefore, the Seto Inland Sea of Japan is under an oligotrophic condition (Yamamoto, 2003; Yamamoto and Hazanato, 2015). In the present study, we estimated that the riverine TP load entering Hiroshima Bay was 1.36 tons P $d^{-1}$, including 440 kg P $d^{-1}$ for the DIP load. This was half that of 880 kg P $day^{-1}$ estimated for 1991 to 2001 by Kittiwanich et al. (2006). Thus, the DIP load from the

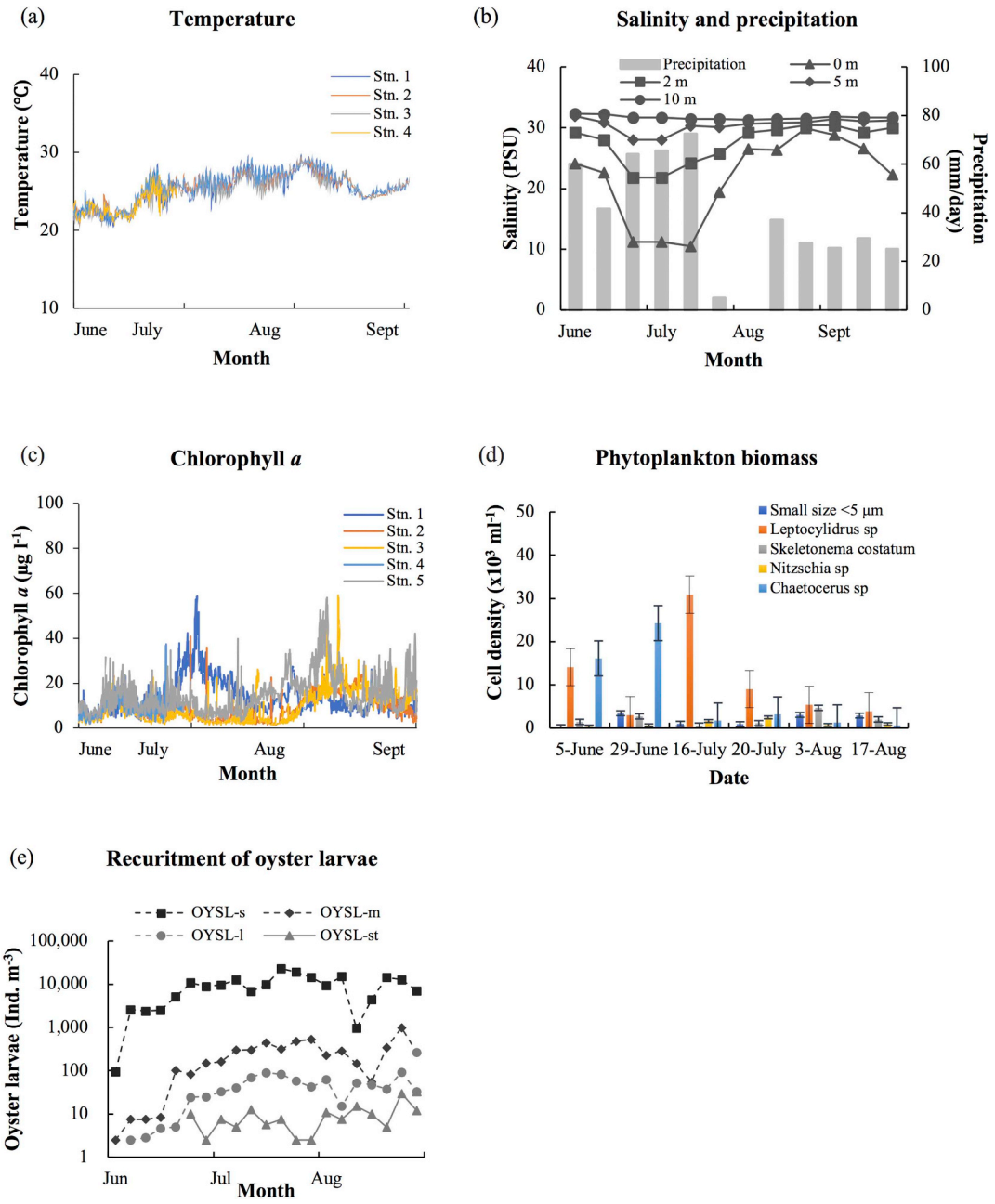


**Fig. 3.** Temporal variations in (a) temperature, (b) salinity and precipitation, (c) chlorophyll *a* fluorescence, (c) phytoplankton species composition and abundance, and (d) average oyster larvae recruitment recorded at five stations in the northern part of Hiroshima Bay from June to September 2016.

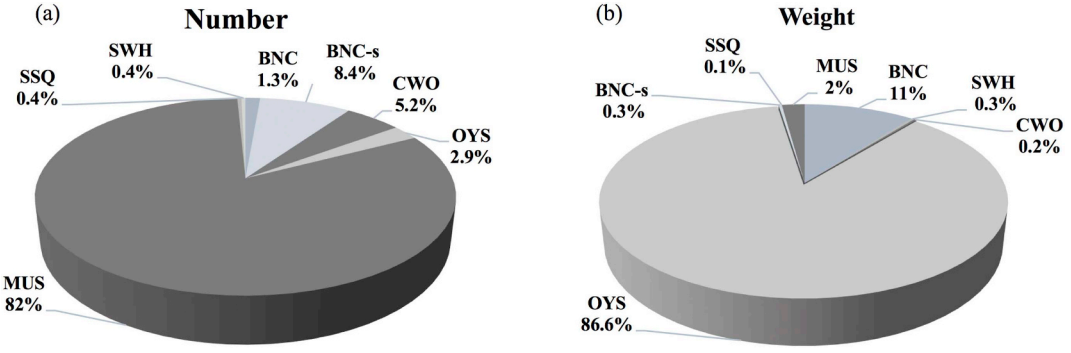


**Fig. 4.** Species composition, in terms of (a) the number of individuals, and (b) wet weight of organisms collected from the oyster rafts. Samples were collected during June to September 2016. MUS is the number of individuals attached to oyster rafts and OYS is highest biomass of all stations.

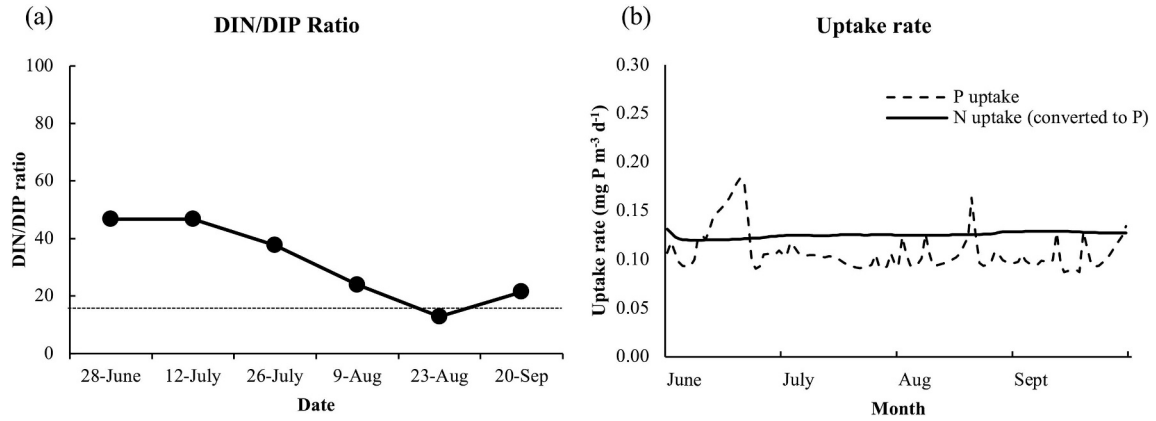


**Fig. 5.** (a) DIN/DIP molar ratio in seawater of Hiroshima Bay, and (b) nutrient uptake rate by phytoplankton. Dissolved inorganic nitrogen (DIN) uptake rate was converted to the equivalent value of dissolved inorganic phosphorus (DIP) divided by the Redfield ratio (16).

river declined from 1.1 mg P $m^{-3}$ in 1990s to 0.2 mg P $m^{-3}$ in 2016. A decrease in NH and NO loads also occurred in Hiroshima Bay. The estimated NH and NO loads were 1.09 and 2.18 mg N $m^{-3}$ $d^{-1}$, which were only half the respective amounts of 3.3 and 5 mg N $m^{-3}$ $d^{-1}$ measured 20 years ago (Kittiwanich et al., 2006). The decrease in nutrients entering the bay has affected environmental conditions, causing low primary production in nHB.

During the observation period, the abundance of PHY-S was extremely low (1.97 cells $\mu l^{-1}$); thus, insufficient amounts of food are available for oyster larvae. Oyster larvae larger than 90 μm at the D-stage can only feed on small-sized phytoplankton, i.e., <5 μm according to Rico-Villa et al. (2006). Food availability affects the development, metamorphosis success, and survival of oyster larvae (Hofmann et al., 2004). According to Rico-Villa et al. (2009), the required phytoplankton density for the development and settlement of Pacific oysters is higher than 20 cells $\mu l^{-1}$. The extremely low PHY-S biomass (1.97 cells $\mu l^{-1}$) observed in this study might be the major cause for the failed recruitment success of oyster larvae in Hiroshima Bay.

### 4.2. Top-down processes

Phytoplankton biomass is controlled by the grazing activity of filter feeders, which is a top-down control process of lower trophic level organisms. Zooplankton in nHB were dominated by copepods, which were the second strongest grazer of phytoplankton, after cultured oysters. According to Alpine and Cloern (1992), copepods graze ca. 50% of phytoplankton biomass per day in San Francisco Bay, USA. Based on our model, the grazing rate of ZOO on PHY-L was 0.41 mg P $m^{-3}$ $d^{-1}$ or 30% per day, which was sufficient to reduce phytoplankton biomass within a day. Thus, ZOO exerts intensive grazing pressure on PHY-L in nHB. The model output also showed a decrease in PHY-L concentration at the end of the modeled period, which might be attributed to intensive grazing.

Cultured oysters (OYS) were the top grazers of PHY-L (0.86 mg P $m^{-3}$ $d^{-1}$), accounting for 66% of total grazing quantity by all filter feeders in the bay. Mussels had the strongest effect in controlling phytoplankton biomass in the Hudson Estuary and San Francisco Bay (USA), with ca. 85% phytoplankton biomass being filtered by mussels (Caraco et al., 1997). In comparison, low amounts of PHY-L were grazed by mussels (0.02 mg P $m^{-3}$ $d^{-1}$) in nHB. Based on our calculations, two times more PHY-L were grazed by oysters compared to zooplankton in nHB, which was consistent with the findings reported by Kittiwanich et al. (2007).

The intensive oyster culture conducted in Hiroshima Bay plays an important role in material cycles via physiological processes. The cultured oysters and other animals attached on oyster rafts were estimated to contribute to a 60% increase of particulate P through the production of feces. Kittiwanich et al. (2006) reported that >80% of DIP input in the upper layer of Hiroshima Bay comes from the internal regeneration processes. Thus, the decomposition of oyster feces is important for regenerating nutrients and enhancing photosynthesis in Hiroshima Bay under present conditions. The decreased in the number of cultured oysters might decrease the contribution of this regeneration process of bio-available nutrients, further decreasing the overall productivity of the bay.

Larviphagy by adult oysters could also have significant impacts because of the huge biomass and feeding activity of adult oysters in nHB. Lehane and Davenport (2005) reported that most mussel larvae were ingested by farmed adult mussels during the spawning season in Ireland. Oyster larvae are also fed on by adult oysters. Tamburri and Zimmer-Faust (1996) estimated in their laboratory experiments that that 77%–92% of veliger larvae of oyster (*Crassostrea virginica*) introduced into the mantle cavity of adult oysters were eaten and digested. At our study site, filtration by adult oysters could contribute to the low survival rates of OYSL-st due to larviphagy. The sensitivity analyses showed a 25% increase in settlement success by decreasing adult oyster biomass to 1/10 of that at present. Our model showed that larviphagy is the second important factor that must be considered in terms of the settlement success of oyster larvae during the planktonic phase.

In our area, foraging by jellyfish could also threaten the survival of oyster larvae. It is reported that bivalve larvae were detected in the gut of *Aurelia aurita*, although the main gut components were copepods and their nauplii (Lo and Chen, 2008). However, we estimated that jellyfish grazed on zooplankton at a rate of 0.05 mg P $m^{-3}$ $d^{-1}$; thus, jellyfish exerted intensive grazing pressure on zooplankton in nHB during the observation period. Although sometimes bivalve larvae were observed to stick to the tentacles of jellyfish (Keesing et al., 2016), the species of larvae could not be identified in the report. In our model, we accounted for the estimated number of larvae consumed by jellyfish. While the amount was not extremely high, there was a loss of oyster larvae to feeding jellyfish.

The area where oysters are cultured appeared to serve as a feeding ground and nursery for several fish species (Matsuda et al., 2000). Tsuyuki and Umino (2017) demonstrated that black sea bream

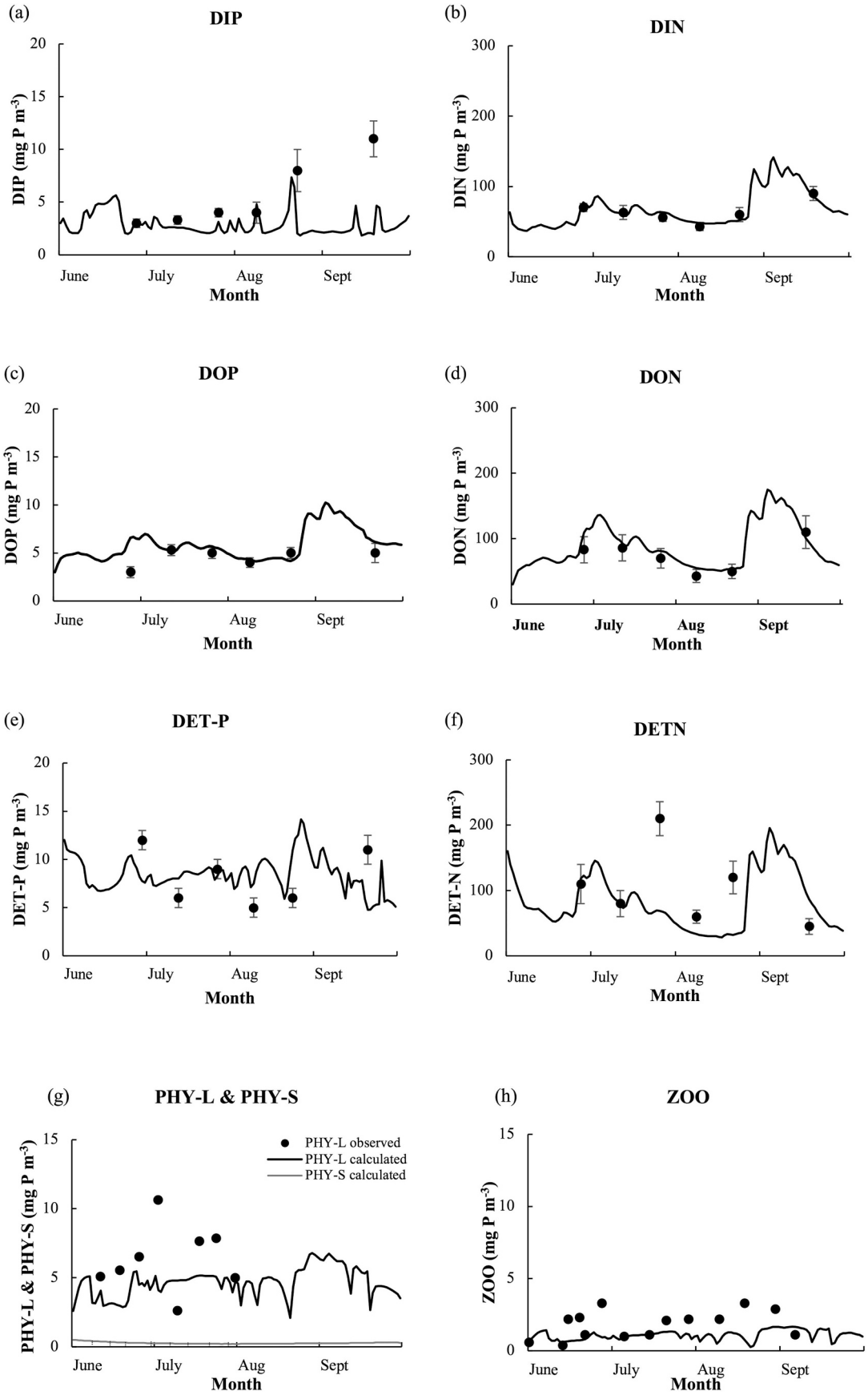


**Fig. 6.** Temporal changes to (a) dissolved inorganic phosphorus (DIP), (b) dissolved inorganic nitrogen (DIN), (c) dissolved organic phosphorus (DOP), (d) dissolved organic nitrogen (DON), (e) detritus phosphorus (DET-P), (f) detritus nitrogen (DET-N), (g) large-sized phytoplankton (PHY-L) and small-sized phytoplankton (PHY-S), (h) zooplankton (ZOO), (i) oysters (OYS), (j-m) oyster larvae at different phases of development (OYSL-s, OYSL-m, OYSL-l, OYSL-st) in the northern part of Hiroshima Bay, where (•) is the observed value and (—) is the calculated value.

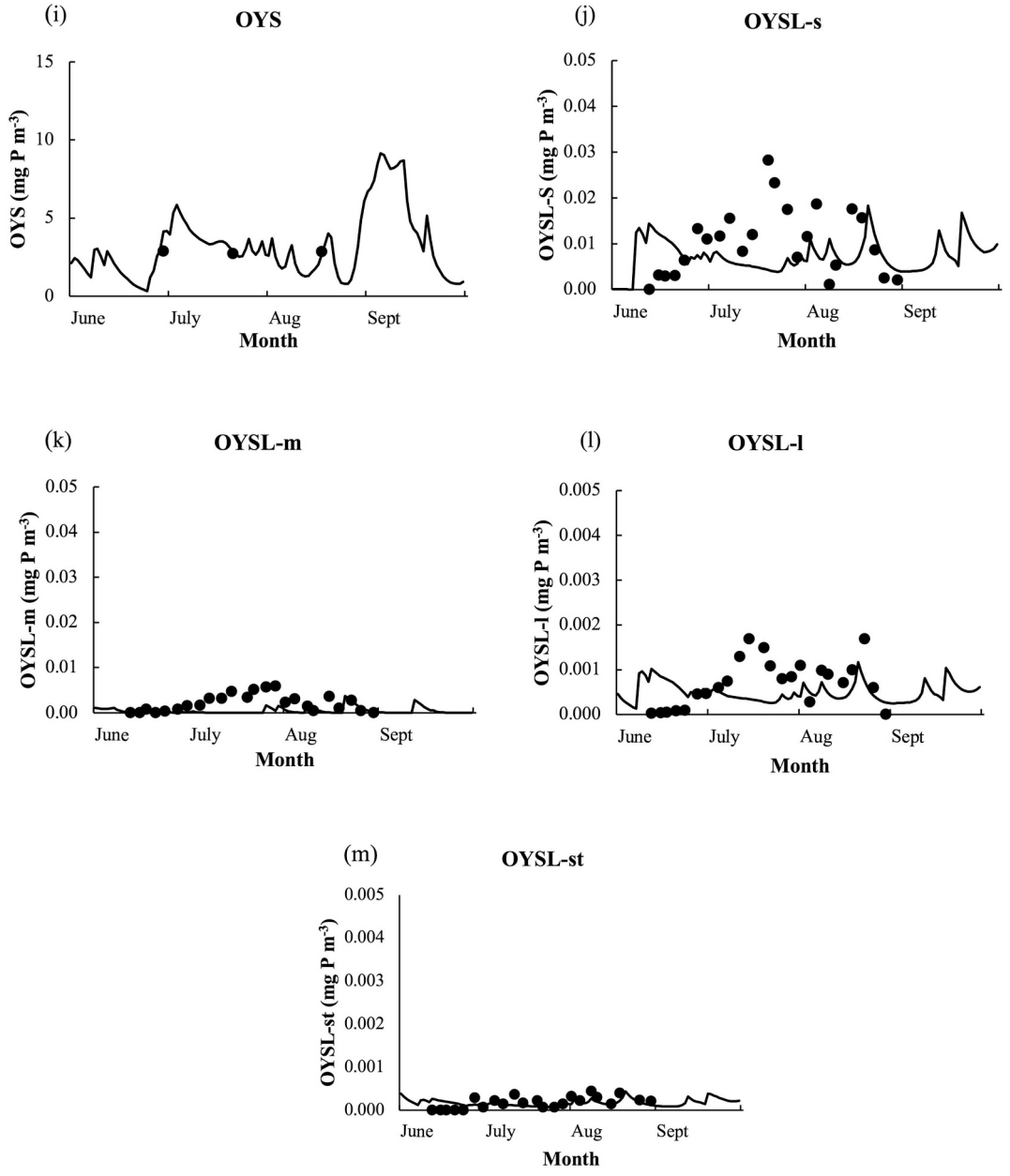


**Fig. 6.** (*continued*)

*Acanthopagrus schlegelii* strongly depended on oyster farms in Hiroshima Bay to feed on animals attached to oyster rafts. Saito et al. (2014) reported the presence of young Pacific oysters and blue mussels in the gut contents of black sea bream and finepatterned puffer *Takifugu poecilonotus*. They feed on only young oysters and blue mussels with soft shells. Thus, the process of oyster feeding by fish was incorporated in our model. However, the fish feeding activity may contribute more to the decline of other attached organisms such as mussels that have softer shells than those of oysters. During the period of eutrophication during 1970s, there was a tremendous number of mussels attached onto oyster culture rafts, but now they have almost disappeared.

Thomas et al. (2015) suggested that the high mortality of oyster larvae before settlement is because of predation by filter feeders in the atoll lagoons of French Polynesia. In our study, when D-type oyster larvae were planktonic, they were filtered by adult oysters at 0.0004, 0.0001, and 0.0001 mg P $m^{-3}$ $d^{-1}$ for every developmental stage (OYSL-s, OYSL-m, and OYSL-l). These values were much smaller than those for the filtration of PHY-L (0.86 mg P $m^{-3}$ $d^{-1}$). Larviphagy may be a significant component in small lagoons, but it makes a comparatively small contribution in terms of driving the low recruitment success of oyster larvae in Hiroshima Bay.

### 4.3. Sensitivity analyses

Low nutrient (P and N) loads theoretically caused primary production in Hiroshima Bay to decline. As shown in the sensitivity analyses, DIP, NH, and NO loads from rivers that are more than five times those at present would cause a 42%, 17%, and 17% increases in

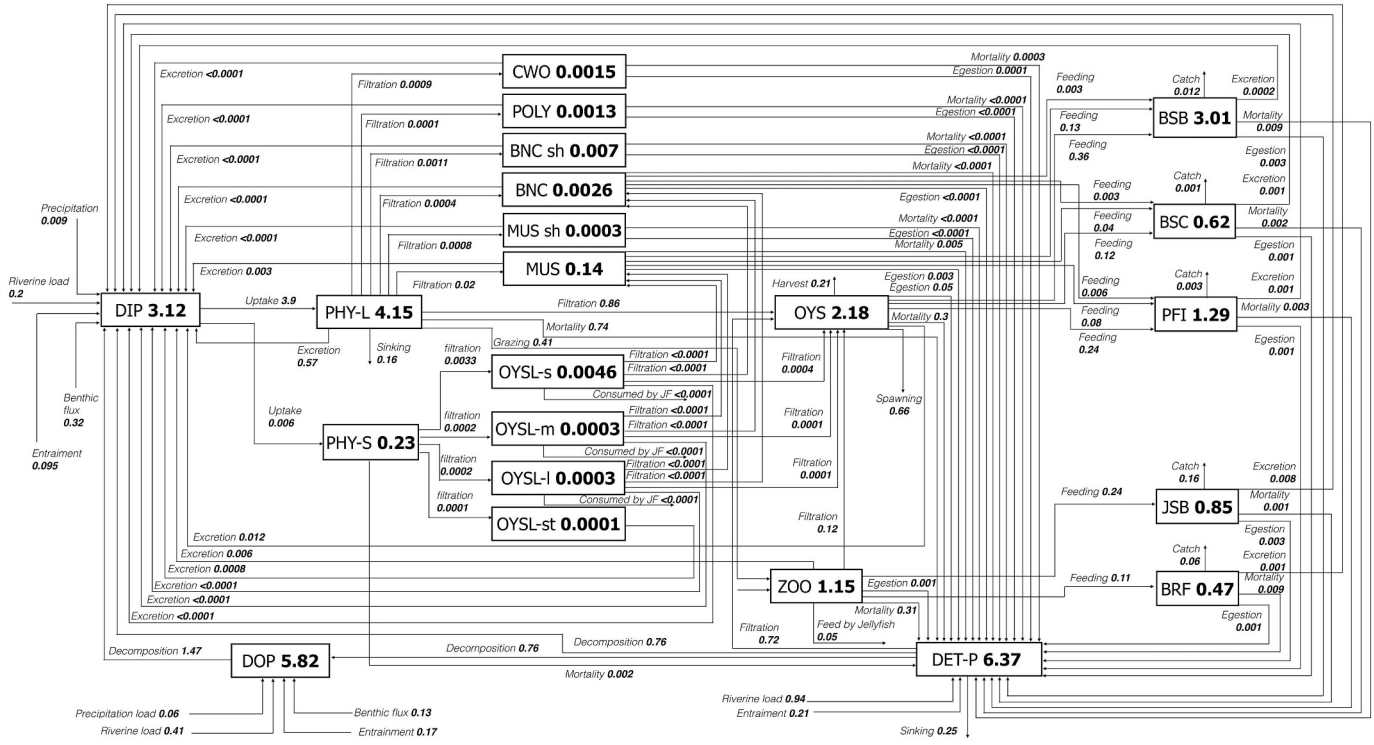


**Fig. 7.** Phosphorus cycles in northern Hiroshima Bay; stock (mg P $m^{-3}$) and fluxes (mg P $m^{-3}$ $d^{-1}$). Abbreviations of stocks are same as those in Fig. 2.

phytoplankton biomass in the bay, respectively. Thus, at present, there are insufficient nutrients, causing a deficiency in small-sized phytoplankton suitable for oyster larvae (Fig. 7). Failed recruitment of oyster larvae was also reported in Oosterschelde Estuary (Netherlands). At this site, the survival of *C. gigas* larvae and/or larval production decreased due to food availability and/or quality dropping below a threshold after 1999, which followed the degradation of water quality in the bay (Troost et al., 2008). In other words, to enhance the recruitment of oyster larvae, it is essential to maintain primary production above a threshold, particularly that of small-sized phytoplankton. This approach would facilitate the growth of oyster larvae during their planktonic phase. Yamamoto et al. (2005) calculated primary production using average DIP loads from 1991 to 2000. Furthermore, Kittiwanich et al. (2006) reported a marked change to phytoplankton biomass in the northern part of Hiroshima Bay, which is directly affected by riverine loads, especially in the upper layer. Our results support these previous studies; however, the depletion in DIP due to legislation has had much more severe consequences on oyster production in the 2010s. Thus, a × 10 increase in the riverine DIP load, which is a quite large input, could counteract presently depleted DIP conditions.

Lowering OYS biomass caused the spawning rate of oysters to decline but increased the recruitment success of oyster larvae by decreasing feeding competition from oysters and other attached animals, in addition to decreasing larviphagy. A decline in OYS biomass to 1/10 of present conditions would cause an increase in both small-sized phytoplankton and oyster larvae of every size. Here, our model takes into account the decrease in spawning resulting from a decrease in oyster adult numbers. Therefore, this could be a "trade-off" between maintaining a harvest of adult oysters and limiting how many larvae fishermen are permitted to collect.

In the nHB, increasing DIP loads ×10 higher increased both the quantity of small-sized phytoplankton and oyster larvae of settling size by 58%. This result was similar to that reported by Kittiwanich et al. (2016), in which phytoplankton biomass increased with increasing nutrient load. The increase of DIP input also had an effect on larger-sized phytoplankton biomass, which is a major food source for oyster growth. From the Redfield ratio (N/P molar ratio = 16), the P uptake rate is lower compared to N uptake rate, which means that P is a limiting factor for phytoplankton growth in our study site. This finding was consistent with that of Yamamoto et al. (2002), who suggested that P was a significant nutrient that regulates phytoplankton growth in Hiroshima Bay. This indicates that Hiroshima Bay has been P-limited for long time and is still P-limited. Compared to the strategy of decreasing oyster biomass, increased nutrient input may prove more effective at sustaining oyster production in Hiroshima Bay.

## 5. Conclusions

The field observations demonstrated that low food availability, particularly of small-sized phytoplankton, which were suitable for oyster larvae, was the primary cause of the failed recruitment of oyster larvae in nHB. The model describing the bottom-up and top-down processes developed in the present study reproduced the material flows in the ecosystem of nHB well. The sensitivity analyses showed that phytoplankton biomass, irrespective of size, increased with increasing nutrient load. Particularly, P was identified as a main limiting factor of phytoplankton growth and also key to the correction of declines in oyster larvae. Although the top-down forces (i.e., larviphagy) could be another potential cause for failed oyster larval recruitment, it was not a significant factor. Thus, we conclude that bottom-up forces, i.e., P in the bay was the main factor, rather than top-down forces, e.g., larviphagy, in determining the successful recruitment of oyster larvae. To maintain

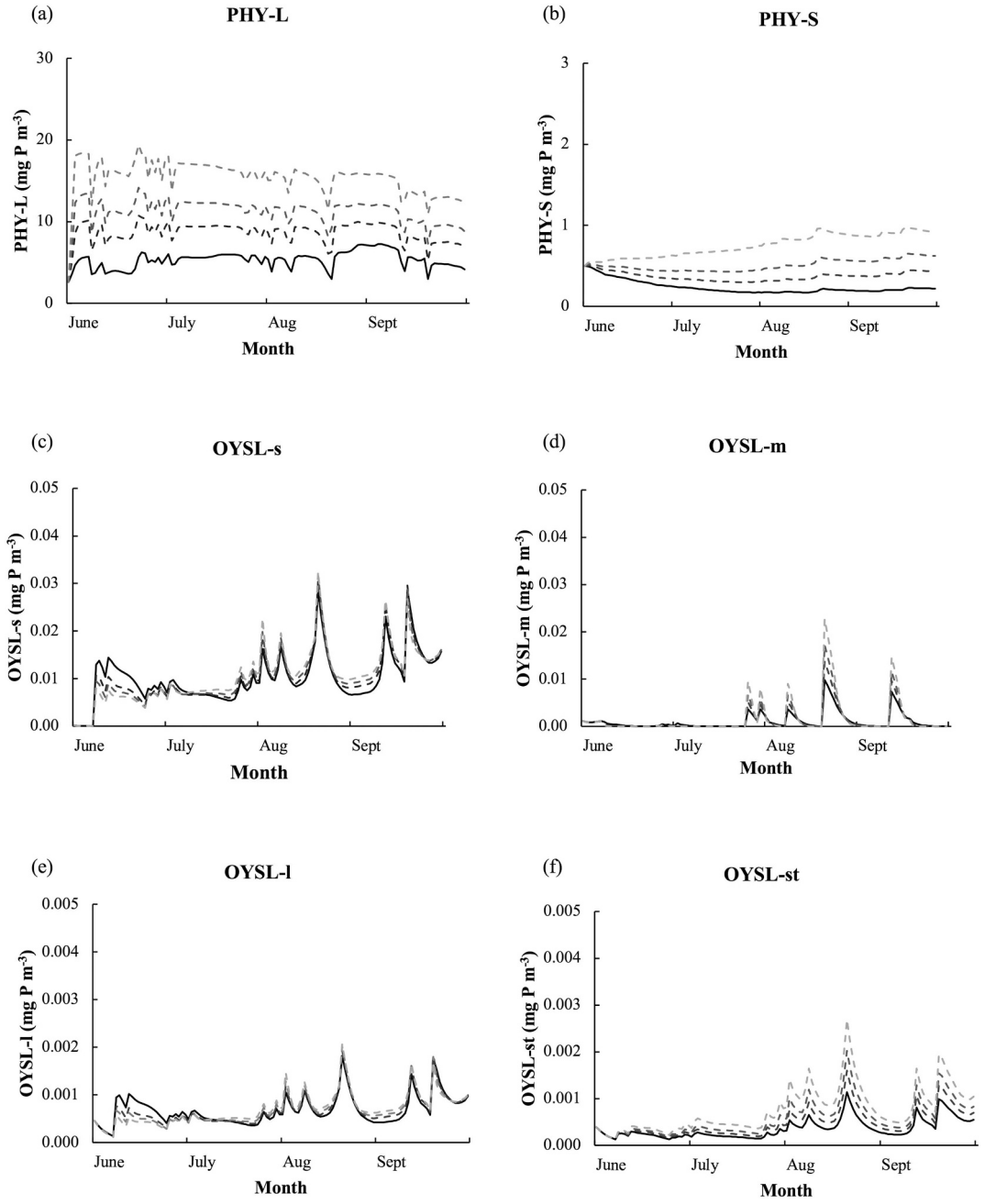


**Fig. 8.** Effect of changing dissolved inorganic phosphorus (DIP) loads on the growth of (a) large-sized phytoplankton, (b) small-sized phytoplankton, and (c)–(f) oyster larvae in different phases of development; −s (small), −m (medium), −l (large) and –st (settling size). The solid line (—) represents the DIP load in 2016, while the dashed lines (…) represent ×2, ×5, and ×10 that of the present DIP load.

larval recruitment at the level required by fishermen, apparently high P loading (ten times higher than the present level) is needed. Relaxation of treated sewage discharge has just started as an oligotrophication measure for the Seto Inland Sea by the local government. We hope that the results from the model developed here could be used to provide a scientific basis for local governments to formulate reasonable measures to maintain oyster bed productivity.

## Declaration of Competing Interest

None.

## Acknowledgments

The first author thanks the Indonesian Endowment Fund for Education (LPDP) for providing financial support for the doctoral scholarship. We also thank Dr. Agung Dharma Syakti for providing valuable suggestions and Dr. Lawrence Manzano Liao for providing

**Table 5**
Effects of increasing nutrients (DIP, NH, NO) loads and decreasing oyster biomass on phytoplankton and oyster larvae in each size category, June to September in northern Hiroshima Bay.

| Parameters for sensitivity analyses | Present value | Increment from the present condition | Compartments (present values) and their response increase | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | PHY-L (5.3 mg P $m^{-3}$) | PHY-S (0.4 mg P $m^{-3}$) | OYSL-s (0.0101 mg P $m^{-3}$) | OYSL-m (0.0006 mg P $m^{-3}$) | OYSL-l (0.0006 mg P $m^{-3}$) | OYSL-st (0.0002 mg P $m^{-3}$) |
| DIP load | 0.2 mg P $m^{-3}$ $d^{-1}$ | ×2 | +33% | +28% | +8% | +23% | +8% | +25% |
| | | ×5 | +46% | +42% | +11% | +35% | +11 | +37% |
| | | ×10 | +58% | +55% | +13% | +48% | +15% | +51% |
| NH load | 1.09 mg N $m^{-3}$ $d^{-1}$ | ×2 | +2% | +10% | +10% | +12% | +9% | +10% |
| | | ×5 | +2% | +17% | +16% | +18% | +15% | +16% |
| | | ×10 | +3% | +21% | +21% | +23% | +20% | +21% |
| NO load | 2.1 mg N $m^{-3}$ $d^{-1}$ | ×2 | +2% | +11% | +11% | +12% | +10% | +11% |
| | | ×5 | +2% | +17% | +16% | +19% | +16% | +17% |
| | | ×10 | +3% | +21% | +21% | +23% | +20% | +21% |
| OYS biomass | 0.14 Ind. $m^{-3}$ | ×1/2 | +3% | +7% | +2% | +3% | +8% | +7% |
| | | ×1/5 | +7% | +14% | +5% | +7% | +12% | +13% |
| | | ×1/10 | +15% | +26% | +6% | +17% | +16% | +25% |

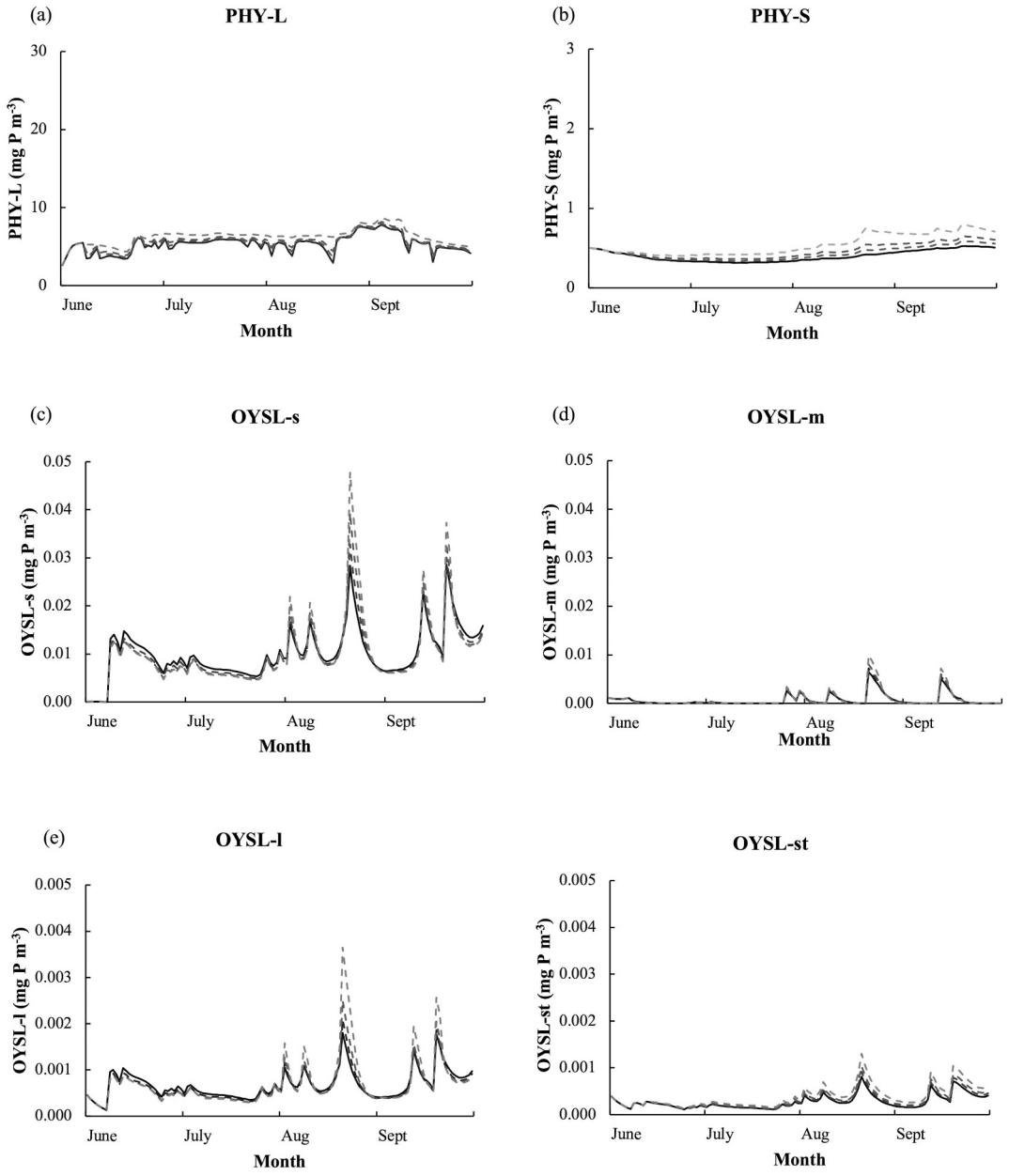


**Fig. 9.** Effect of changing OYS biomass on the growth of (a) large-sized phytoplankton, (b) small-sized phytoplankton and (c)–(f) oyster larvae in different phases of development; the size category is the same as in Fig. 8. The solid line (—) represents the OYS biomass in 2016, while the dashed lines (…) represent that of ×1/2, ×1/5, and ×1/10 of OYS biomass.

comments and corrections on our manuscript. This study was carried out under the collaborative research program among Hiroshima City, Hiroshima Prefecture and Hiroshima University with financial support from Hiroshima University. The Hiroshima City Fisheries Promotion Center provided the vessel and help with field observations.

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