



Kelp cultivation effectively improves water quality and regulates phytoplankton community in a turbid, highly eutrophic bay

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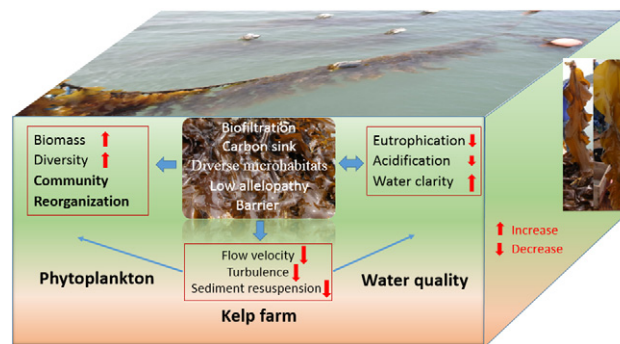
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HIGHLIGHTS

- Kelp farming alleviated eutrophication and acidification.
- Kelp farming greatly relieved light limitation and increased phytoplankton biomass.
- Kelp farming appreciably enhanced phytoplankton diversity.
- Kelp farming reduced the dominance of dinoflagellate *Prorocentrum minimum*.
- Phytoplankton community differed significantly between the kelp farm and control area.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 19 September 2019

Received in revised form 11 November 2019

Accepted 14 November 2019

Available online 18 November 2019

Editor: Jay Gan

Keywords:

Kelp cultivation

Eutrophication

Acidification

Phytoplankton community

Harmful algal blooms

Xiangshan Bay

ABSTRACT

Coastal eutrophication and its associated harmful algal blooms have emerged as one of the most severe environmental problems worldwide. Seaweed cultivation has been widely encouraged to control eutrophication and algal blooms. Among them, cultivated kelp (*Saccharina japonica*) dominates primarily by production and area. However, the responses of water quality and phytoplankton community to kelp farming remain unclear. Here, thirteen cruises were conducted in the kelp farms and control areas in the turbid, highly eutrophic Xiangshan Bay of the East China Sea from 2008 to 2015. Results indicated that kelp cultivation slightly increased dissolved oxygen and pH, but reduced dissolved inorganic nitrogen and phosphorus. We estimated that kelp harvesting would remove 297 t of nitrogen and 42 t of phosphorus from this bay annually. Because of decreased flow velocity, turbulence, and sediment resuspension, kelp farming greatly reduced suspended solids and increased transparency, resulting in increases in phytoplankton chlorophyll *a* and abundance. Additionally, kelp farming appreciably increased phytoplankton species number, Marglef richness, and Shannon–Wiener diversity indices by 51.6%, 40.1%, and 13.1%, respectively. Analysis of similarity and similarity percentages demonstrated that phytoplankton community composition differed significantly between the farm and control area, which was mostly attributed to long-chained diatoms and single-celled dinoflagellates. However, after the kelp harvesting, all measurements of water quality and phytoplankton biomass, diversity, and community composition exhibited no

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significant difference. Our study highlights that kelp cultivation alleviates eutrophication and acidification and enhances phytoplankton diversity, thus providing guidance for macroalgal aquaculture and remediation in eutrophic waters.

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1. Introduction

During previous decades, nitrogen (N) and phosphorus (P) input into coastal waters, particularly estuaries and bays, have increased sharply due to increased economic activity and an enlarged human population. Coastal nutrient overenrichment has resulted in increased phytoplankton biomass and harmful algal blooms (HABs; Anderson et al., 2002; Jiang et al., 2014; Glibert et al., 2018). Anthropogenic eutrophication, and its consequent exacerbation of HABs, has resulted in a chain of ecological and socioeconomic effects on coastal waters, such as on water quality, fisheries, tourism, the ecosystem, and public health (Bricker et al., 2008; Paerl et al., 2018); it is a highly severe global environmental problem (Glibert et al., 2018). Effectively alleviating eutrophication and controlling HABs has thus become a major challenge facing government and academia.

Seaweeds (macroalgae) grow by photosynthesis by absorbing dissolved nutrients in coastal waters, thus competing with microalgae for resources, such as nutrients and light (Smith and Horne, 1988; Gross, 2003; Yang et al., 2015a). The harvest of seaweeds is a net removal of nutrients from coastal waters (Xiao et al., 2017; Yang et al., 2015a), which efficiently reduces N and P availability for phytoplankton growth and thus indirectly alleviates HABs (Yang et al., 2015a, 2015b). Furthermore, seaweeds may suppress phytoplankton photosynthesis and growth and mitigate algal blooms by allelopathic inhibition and shading (Gross, 2003; Yang et al., 2015a). Therefore, seaweed cultivation has been widely proposed as an ecological restoration tool to perennially control eutrophication and HABs (Buschmann et al., 2001, 2017; Chung et al., 2002; Neori et al., 2004; Yang et al., 2015a, 2015b; Seghetta et al., 2016; Kim et al., 2017; Xiao et al., 2017). Until now, most bioremediation studies have focused on nutrient removal efficiency or the potential of cultivated seaweeds, such as green algae of *Ulva* (Mariachiaro and Pierluigi, 2002), red algae of *Gracilaria/Gracilariopsis* (Marinho-Soriano et al., 2009; Mao et al., 2009; Yang et al., 2015a; Huo et al., 2011; Huang et al., 2017) and *Pyropia* (He et al., 2008), and brown algae of *Saccharina* (Xu et al., 2011; Marinho et al., 2015; Seghetta et al., 2016). However, the effects of seaweed cultivation on phytoplankton biomass and community structure in natural waters remain poorly documented, as a measurable impact requires large-commercial scale of seaweed farming.

Seaweed cultivation has burgeoned over the past decades, mostly in Asia and more recently in Europe and the Americas (Buschmann et al., 2001, 2017; Kim et al., 2017). As a source of food, medicament, and biofuels, seaweeds have economic value in addition to their ecological function (Buschmann et al., 2017; Kim et al., 2017; FAO, 2018; Zhang and Thomsen, 2019). This strongly encourages their cultivation in coastal waters. China is the biggest seaweed culturing country, contributing 47.9% to global production in 2016 (FAO, 2018). Among them, kelp (*Saccharina japonica*) dominates primarily by cultivated production and area. In 2018, its farming production and area in China were 2,343,871 t (dry weight) and 45,100 ha, respectively, accounting for 65.0% and 31.3% of China's seaweed cultivation production and area (China Fisheries Statistical Yearbook (CFSC), 2019). Evaluating the remediation effectiveness of kelp cultivation in alleviating eutrophication and HABs is therefore necessary. Several studies have demonstrated that *Gracilaria/Gracilariopsis*, ranking at third in seaweed production in China (China Fisheries Statistical Yearbook (CFSC), 2019), may significantly remediate nutrient contamination in mariculture ecosystems and improve the water environment (Huo et al., 2011, 2012; Yang et al., 2015a; Huang et al., 2017). However, to the best of our knowledge,

the effect of kelp cultivation on the water quality and phytoplankton community has not been systematically investigated.

Earlier filed studies have usually observed negative correlations between the abundance of phytoplankton and macroalgae in coastal waters (Smith and Horne, 1988; Sfriso et al., 1989), a distribution pattern likely due to competition for nutrient acquisition and absorption (Smith and Horne, 1988; Fong et al., 1993). Recently, a large body of literature has demonstrated that many species of red, green, and brown macroalgae release allelochemicals that inhibit microalgal photosynthesis and growth in the laboratory, particularly that of HAB dinoflagellates and diatoms (Jeong et al., 2000; Nan et al., 2004; Tang and Gobler, 2011; Han et al., 2013; Ye et al., 2014; Tang et al., 2015; Yang et al., 2015b). Previous studies have suggested that seaweed cultivation significantly reduces phytoplankton abundance (Huo et al., 2011; Yang et al., 2015a; Huang et al., 2017) and largely enhances plankton biodiversity (Huo et al., 2011; Jiang et al., 2012; Chai et al., 2018). Therefore, we hypothesize that the phytoplankton community is largely shaped by kelp farming, including decreased biomass and increased diversity.

To test this hypothesis, thirteen cruises were conducted in the kelp farms (KFs) and control areas (CAs) of Xiangshan Bay (XSB) from 2008 to 2015. Among these cruises, seven were conducted during the kelp culture period (during winter and spring) and six after the kelp harvesting (during summer and autumn). We examined how kelp farming influences the water quality and phytoplankton community. Our objectives were (1) to determine the effects of kelp farming on water quality, (2) to explore the effects of kelp farming on phytoplankton biomass and community structure, and (3) to evaluate the bioremediation potential and efficiency of kelp farming in this bay. Our study is useful to those seeking to understand the environmental and ecological effects of kelp farming and serves as a guide to future policy making on aquaculture and ecological restoration in coastal eutrophic waters.

2. Materials and methods

2.1. Study area and sampling dates

XSB is a subtropical semi-enclosed bay located in Ningbo city, northern Zhejiang Province, China (Fig. 1). It is a long (ca. 60 km), narrow (ca. 3–8 km), and shallow (~10 m depth) bay typical of those in the East China Sea. The upper and middle sections of this bay have long residence times of approximately 80 and 65 days, respectively, with 90% water exchanges (Ning and Hu, 2002). The average tidal range is ~3 m with a maximum up to 5.7 m (Ning and Hu, 2002), whereas the average surface tidal current velocity in the middle bay during the neap and spring tides are 17–37 and 43–67 cm/s, respectively (Editorial Committee of the Bay Chorography in China ECBCC, 1992). Because of low water-exchange, XSB is subjected to severe eutrophication caused by industrial and agricultural sewage discharge and excessive mariculture (Ning and Hu, 2002; Huang et al., 2008; Jiang et al., 2012, 2019b). However, the chlorophyll *a* (chl_a) was low with a seasonal average concentration of 2.02 µg/L, largely because of light limitation from strong tide-induced sediment resuspension (Jiang et al., 2019b, 2019c).

The kelp (*S. japonica*) in XSB has been cultivated since the 1960s, coinciding with burgeoning seaweed cultivation in China. The present cultivation area and production in this bay are exceeds 700 ha and 8000 t (dry weight), respectively. The cultivated kelp is a temperate species, which is usually seeded during November and harvested during late April to early May in the following year, at water temperatures of <20 °C. The kelp is tied to ropes, and it grows downward in the upper

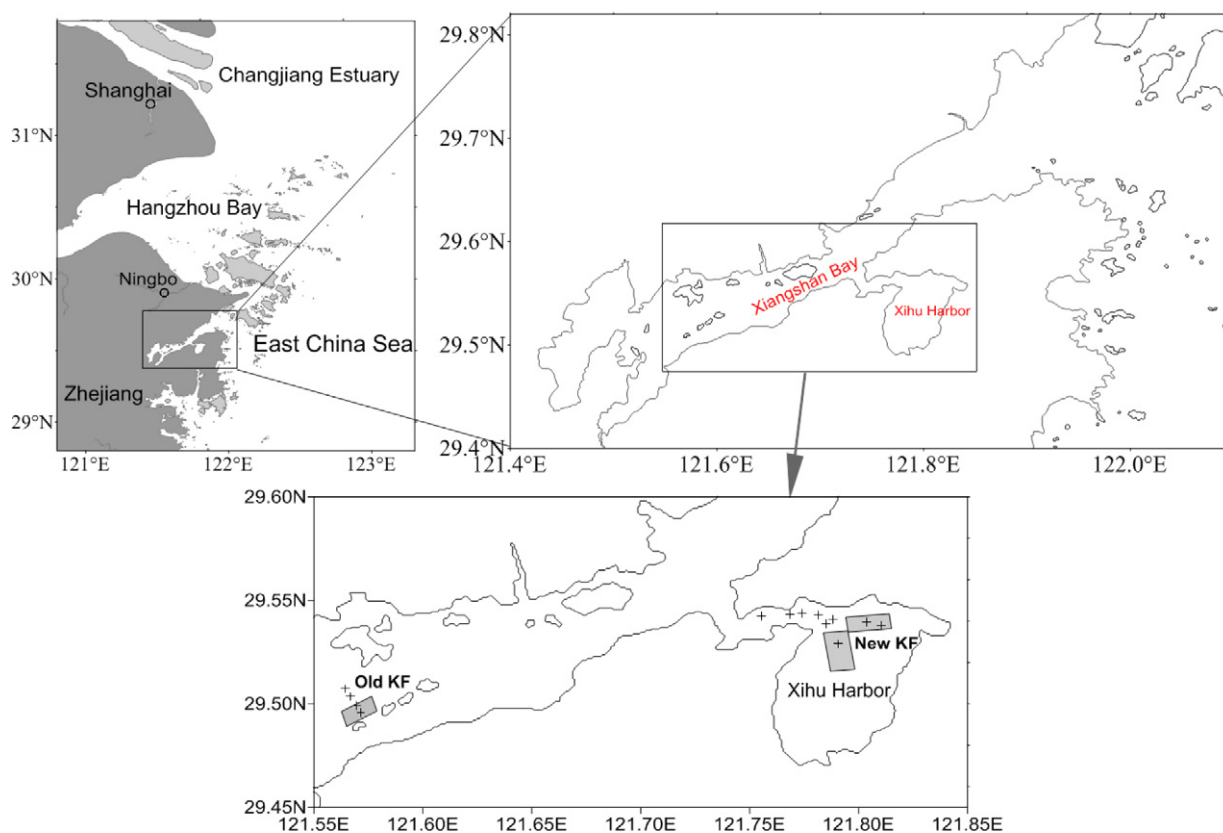


Fig. 1. Diagram of sampling stations (cross) in the old (during 2008–2010) and new (during 2015) kelp farm (KF) in Xiangshan Bay. The grey rectangles in the middle bay and Xihu Harbor indicate location of the old and new KF, respectively.

water column (Fig. S1). The length of kelp thallus during the harvested period typically ranges from 1 to 2 m. To investigate the effects of the presence/absence of kelp farming on the water quality and phytoplankton community, seven cruises were conducted in KFs and CAs during the kelp culture period (on December 31, 2008, March 1, 2009, April 8, 2009, January 30, 2010, April 25, 2010, January 21, 2015, and April 26, 2010), and six cruises were conducted after the kelp harvesting (on May 21, 2009, August 05, 2009, July 14, 2010, November 17, 2010, July 18, 2015, and October 15, 2015). Among these cruises, nine from 2008 to 2010 were in the old KF (~20–50 ha) and the adjacent CA in the middle bay. Thereafter, the old KF was removed, and four cruises were conducted in 2015 in the new KF (~200 ha) and the adjacent CA in a branched bay (Xihu Harbor). Fig. 1 shows sampling areas and stations in XSB. From 2008 to 2010, 1–2 sampling stations were set in both KF and CA (500–1000 m apart from the farm edge). In 2015, three stations were setting in KF, and six stations were set in CA. Table S1 shows sampling strategies of water quality and phytoplankton during the kelp culture period and after the kelp harvesting. The average water depths in the old and new farms were 8 and 12 m, respectively.

2.2. Environmental parameters and phytoplankton

Surface (0.5 m depth) and bottom (0.5 m above the seabed) seawater at each station were collected in 5-L Niskin bottles. Temperature and salinity were measured in situ with a YSI model 30 salinity meter, and transparency was measured with a Secchi disc. Dissolved oxygen (DO) was measured with Winkler titrations, and pH was measured with an Orion 868 pH meter. To measure other parameters, including dissolved inorganic nitrogen (DIN), phosphorus (DIP), silicate (DSi), chl_a, and suspended solids, water samples filled in 5-L buckets were preserved in dark and deep frozen surroundings before the laboratory operation. The methods of pretreatment and determination on nutrients and suspended solids have been described in Jiang et al. (2019c).

Water samples (100 mL) that were collected between 2008 and 2010 for total chl_a were filtered through a 0.7- μm GF/F filters (Whatman). In 2015, size-fractionated chl_a was measured in each season. Chl_a was size fractionated into micro (>20 μm), nano (2–20 μm), and picophytoplankton (<2.0 μm) by filtering water samples through three types of filters (20, 2, and 0.7 μm). The methods of filtering and determination on chl_a have been described in Jiang et al. (2019b). From 2008 to 2010, three water samples for phytoplankton analysis were collected from the surface and bottom at each station. In 2015, one phytoplankton sample was collected from each layer. The processes of preservation, sedimentation, and identification for phytoplankton samples have been described previously (Jiang et al., 2019a, 2019c).

2.3. Data analysis

The species number (S), Marglef richness (d), Shannon–Wiener diversity (H'), and Pielou evenness (J') indices of phytoplankton were calculated with PRIMER 5.0. Partial data on environmental (transparency, suspended solids, temperature, salinity, and nutrients) and phytoplankton (chl_a, abundance, and S) parameters on March 1, 2009, January 30, 2010, and April 25, 2010 have been described previously (Jiang et al., 2012). A two-way (area and water layer) Scheirer-Ray-Hare test (non-parametric analysis of variance) using the package “rcompanion” in software R v3.6.1 (<https://www.R-project.org>) was applied to test for significant differences in phytoplankton and physicochemical variables (except transparency) on different dates. A Kruskal–Wallis test was performed to reveal significant difference of transparency between KF and CA. Because phytoplankton and environmental parameters varied non-significantly between layers in most cases (Tables S2–S4), their average values in KF and CA were depicted using SigmaPlot 10.0 to better illustrate the effects of kelp cultivation. Analysis of similarity (ANOSIM) and similarity percentages (SIMPER) in PRIMER 5.0 were performed to determine difference in the phytoplankton community between KF and

CA. These analyses were conducted based on $\log(x + 1)$ -transformed abundance data by using the Bray–Curtis similarity.

3. Results

3.1. Physicochemical parameters

Temperature and salinity ranged from 10.4 to 29.1 °C and 18.8 to 26.1, respectively. No significant difference in temperature and salinity was found between KF and CA in all cases (Fig. 2; Table S2). Kelp farming slightly, and in some cases, significantly ($p < 0.05$) increased DO (by 1.0%) and pH (by 0.15%). Transparency ranged from 0.15 to 2.50 m (Fig. 2). During the kelp culture period, transparency was significantly ($p < 0.05$) higher in KF than in CA, whereas suspended solids was significantly ($p < 0.05$; in some cases) lower in KF than in CA. Concentrations of DIN, DIP, and DSi were lower in KF than in CA, although no significant difference was found in most cases. On average, kelp farming greatly increased transparency by 32.7% and reduced suspended solids, DIN, DIP, and DSi by 32.9%, 5.8%, 2.5%, and 2.2%, respectively (Table 1). However, after the kelp harvesting (removal of cultivated rafts), all these physicochemical variables exhibited no significant difference between original KF and CA in all cases.

3.2. Phytoplankton abundance and chl_a

Phytoplankton abundance (cells/mL; Fig. 3a) and chl_a concentration (Fig. 3b) were usually higher in KF than in CA during the kelp culture period. In some cases, a significant ($p < 0.05$) difference between KF and CA was found (Table S2). Kelp farming increased phytoplankton abundance and chl_a concentration by an average of 35.3% and 11.6%, respectively (Table 1). However, after the kelp harvesting, phytoplankton abundance and chl_a concentration differed slightly between KF and CA (Fig. 3; Table 1). Phytoplankton size structure indicated that micro- and nano-chl_a contributed >85% to total chl_a; no significant difference in size-fractionated chl_a contribution was found between KF and CA (Fig. S2; Table S3).

3.3. Phytoplankton diversity

Phytoplankton diversity indices (S , d , H' , and J') varied significantly ($p < 0.05$; in most cases) between KF and CA during the kelp culture period (Fig. 4; Table S4). All diversity indices except J' were higher in KF than in CA in most cases. Kelp farming increased S , d , H' , and J' by 51.6%, 40.1%, 13.1%, and -0.2% on average, respectively (Table 1). However, after the kelp harvesting, diversity indices differed slightly between KF and CA (Table S4).

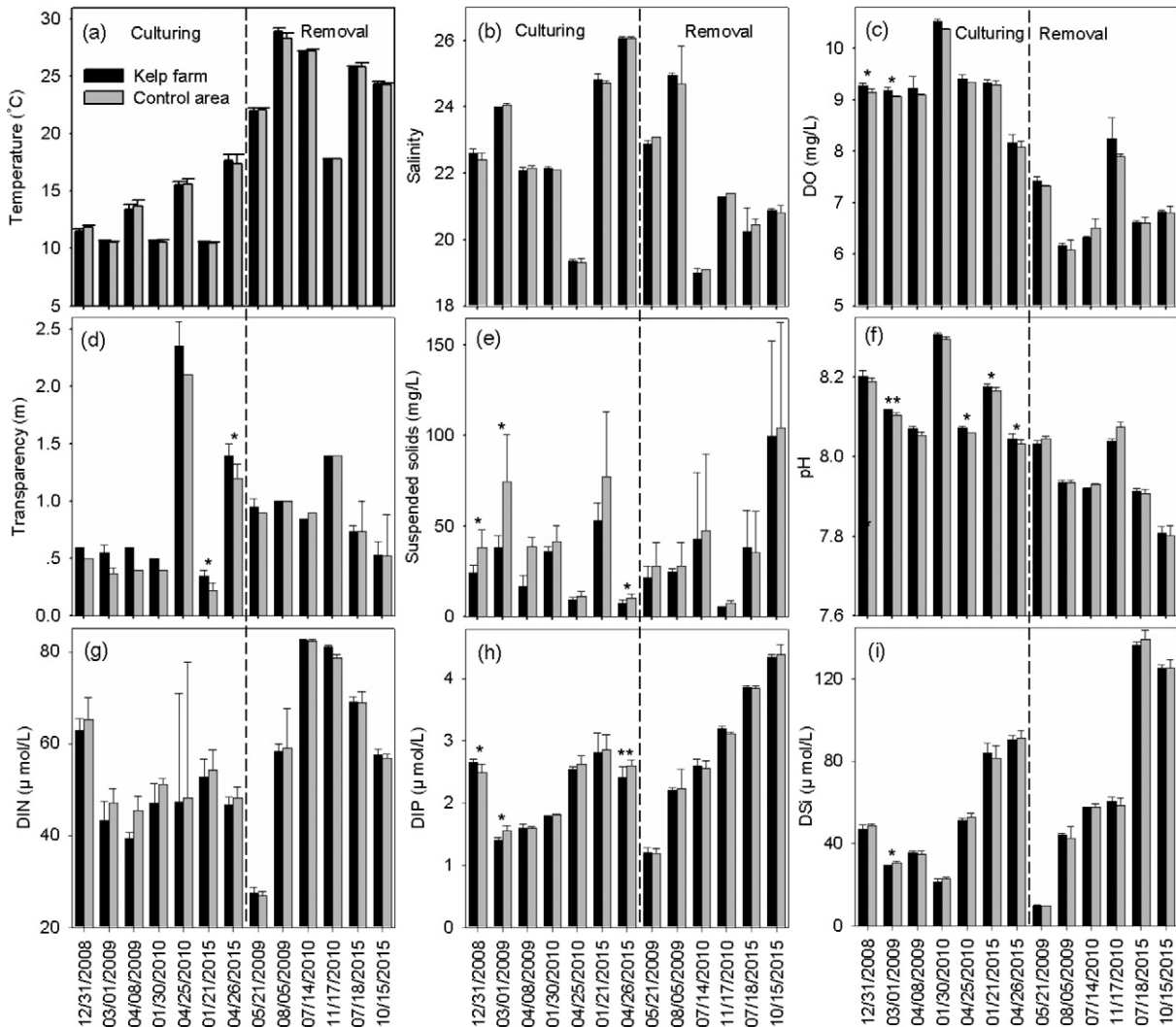


Fig. 2. (a) Temperature, (b) salinity, (c) dissolved oxygen (DO), (d) transparency, (e) suspended solids, (f) pH, (g) dissolved inorganic nitrogen (DIN), (h) phosphorus (DIP), and (i) silicate (DSi) in the kelp farm and control area during the kelp culture period and after the kelp harvesting (removal of the kelp rafts).

Table 1

Increased percentage (%) of phytoplankton and environmental parameters in the kelp farm compared with the control area on different dates. Tran: transparency; SS: suspended solids; DO: dissolved oxygen; DIN: dissolved inorganic nitrogen; DIP: dissolved inorganic phosphorus; DSi: dissolved silicate; Chla: chlorophyll a; Abun: abundance; S: species number; d: Marglef richness index; H': Shannon–Wiener diversity index; J': Pielou's evenness index. Superscripted lower-case letters of different dates indicate presence/absence of the kelp cultivation. ^a: during the kelp culture period; ^b: after the kelp harvesting.

Date	Tran	SS	DO	pH	DIN	DIP	DSi	Chla	Abun	S	d	H'	J'
12/31/2008 ^a	20.0	-37.1	1.5	0.15	-3.7	6.4	-3.3	48.8	166.8	47.1	19.8	-12.9	-21.6
03/01/2009 ^a	50.0	-48.4	1.2	0.19	-8.3	-9.9	-4.0	15.9	-11.2	46.2	32.8	-9.6	-17.7
04/08/2009 ^a	50.0	-56.7	1.5	0.19	-13.2	0.2	1.3	-1.1	-0.2	35.8	38.0	-10.7	-18.4
01/30/2010 ^a	25.0	-13.6	0.7	0.09	-7.8	-1.6	-8.1	8.4	14.7	71.6	66.7	24.7	4.7
04/25/2010 ^a	11.9	-16.2	0.8	0.16	-2.0	-3.4	-3.3	4.0	86.6	97.2	57.2	53.4	22.2
01/21/2015 ^a	55.6	-31.4	0.4	0.11	-2.5	-1.8	3.0	9.7	12.3	30.7	22.9	10.8	3.1
04/26/2015 ^a	16.7	-27.0	1.1	0.14	-2.8	-7.7	-1.2	-4.5	-22.0	32.5	43.2	36.1	26.4
Average ^a	32.7	-32.9	1.0	0.15	-5.8	-2.5	-2.2	11.6	35.3	51.6	40.1	13.1	-0.2
05/21/2009 ^b	5.6	-5.9	1.4	-0.16	1.6	1.0	3.0	11.5	-5.5	-1.6	-0.1	-0.4	-0.7
08/05/2009 ^b	0.0	7.3	1.5	0.00	-1.2	-1.3	4.4	-1.6	0.8	2.7	8.1	9.5	8.8
07/14/2010 ^b	-5.6	1.4	-0.5	-0.13	0.2	1.6	0.4	-1.9	7.6	0.7	-5.0	0.4	0.2
11/17/2010 ^b	0.0	-5.8	-0.5	-0.15	3.1	2.5	3.5	4.3	20.0	-4.5	-10.3	-7.1	-5.9
07/18/2015 ^b	0.0	7.4	-1.0	0.06	0.4	0.2	-2.0	-3.4	-9.6	-7.3	-2.6	-0.4	1.4
10/15/2015 ^b	1.6	-4.3	0.3	0.09	1.4	-0.9	0.1	-7.2	9.1	3.6	2.9	-1.0	-1.8
Average ^b	0.3	0	0.2	-0.05	0.9	0.5	1.6	0.3	3.7	-1.1	-1.2	0.2	0.3

Bold fonts indicate the average values of phytoplankton and environmental parameters during the kelp culture period and after the kelp harvesting.

3.4. Dominant phytoplankton species/genera

During the kelp culture period, dominant species/genera were diatoms (*Skeletonema*, *Thalassiosira*, *Chaetoceros*, *Coscinodiscus*, *Cyclotella*, *Ditylum brightwellii*, *Guinardia delicatula*, *Navicula corymbosa*, *Nitzschia*, *Melosira/Paralia*, and *Pleurosigma*), dinoflagellate (*Prorocentrum minimum*), euglenophyte (*Eutreptia lanowii*), and cryptophyte (unidentified species with cell size of <10 μm). The dominance of long-chained planktonic (e.g., *Skeletonema*, *Thalassiosira*, and *G. delicatula*) and epiphytic (*N. corymbosa* and *Pleurosigma*) diatoms were usually higher in KF than in CA, whereas benthic (*Nitzschia* and *Melosira/Paralia*) and large-celled planktonic (*Coscinodiscus* and *Cyclotella*) diatoms and small single-celled species (*P. minimum* and cryptophytes) were lower in KF than in CA (Fig. 5).

3.5. ANOSIM and SIMPER of phytoplankton community

A two-way ANOSIM indicated a significant ($p < 0.01$) difference in phytoplankton community composition between KF and CA during the kelp culture period despite the water layer difference (Table 2). However, after the kelp harvesting, no significant regional difference in phytoplankton community was found. This finding suggests that

kelp farming significantly influenced phytoplankton community composition. According to SIMPER results, long-chained (*Skeletonema*, *Thalassiosira*, *G. delicatula*, and *Chaetoceros*), large-celled (*Coscinodiscus*, *D. brightwellii*, and *Actinocyclus ehrenbergii*) planktonic diatoms, benthic and epiphytic diatoms (*Cylindrotheca closterium*, *Melosira moniliformis*, *N. corymbosa*, *Paralia sulcata*, and *Pleurosigma aestuarii*), and small single-celled dinoflagellates (*P. minimum*, *Gymnodinium* spp., *Karlodinium veneficum*, and *Scrippsiella trochoidea*) and other groups (*E. lanowii* and unidentified cryptophyte and chlorophyte species) were responsible for this difference (Table S5).

4. Discussion

4.1. Improvement of water clarity by kelp farming

XSB has a large tidal range and a high tidal current velocity, resulting in strong tide-induced sediment resuspension (Editorial Committee of the Bay Chorography in China ECBC, 1992; Ning and Hu, 2002). The present study areas were characterized by relatively low transparency of 0.86 m (ranging from 0.15 to 2.50 m) and high suspended solids at 36.3 mg/L (Fig. 2d, e). During the kelp culture period, transparency (suspended solids) was significantly ($p < 0.05$; in some cases) higher

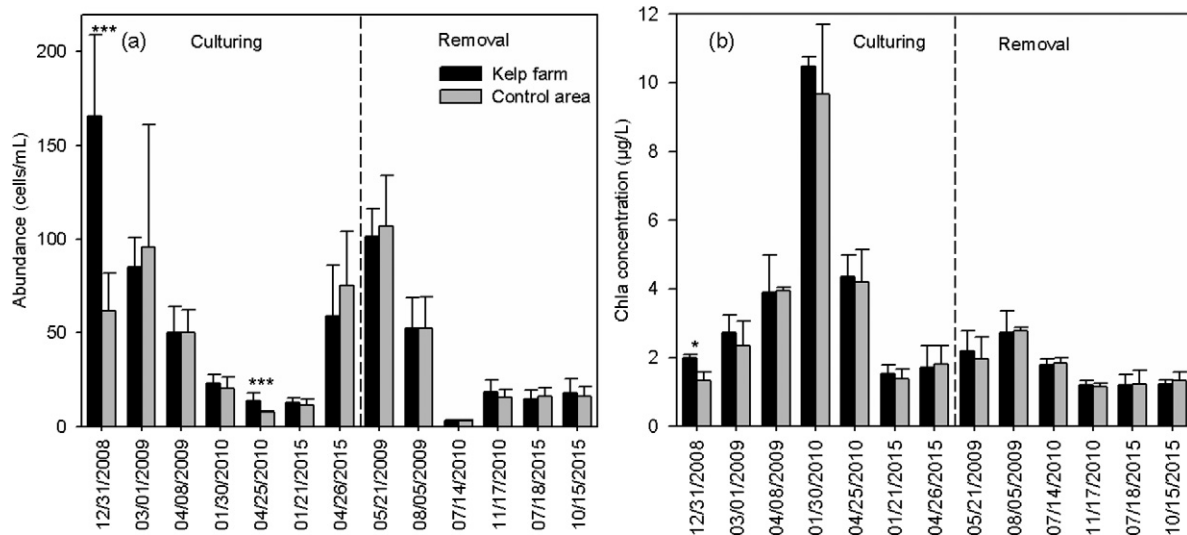


Fig. 3. Phytoplankton (a) abundance and (b) chlorophyll a (chla) concentration in KF and CA during the kelp culture period and after the kelp harvesting (removal of the kelp rafts).

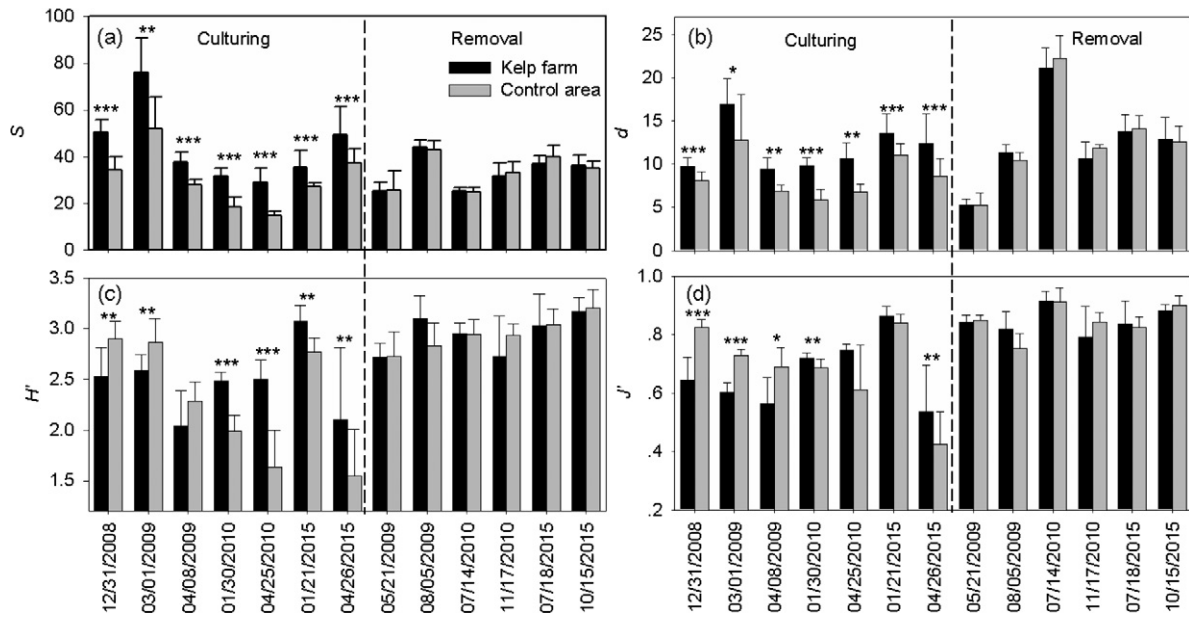


Fig. 4. (a) Species number (S), (b) Margalef richness (d), (c) Shannon–Wiener diversity (H'), and (d) Pielou evenness (J') indices of phytoplankton in the kelp farm and control area during the kelp culture period and after the kelp harvesting (removal of the kelp rafts).

(lower) in KF than in CA. This finding was consistent with a previous study on a *Gracilaria* farm (Zhang et al., 2018).

Previous studies have demonstrated that seaweed cultivation effectively reduced flow velocity and turbulence because of culture rafts on the surface and the dense macroalgal thallus in the upper water column (Hurd, 2010; Grant and Bacher, 2001; Shi et al., 2011; He et al., 2016; Zhang et al., 2016). In Sungo Bay, kelp farming reduced surface current velocity by 30%–78% (He et al., 2016). In Heini Bay, kelp farming largely weakened the bottom shear stress of the seabed boundary layer, which restrained sediment resuspension and reduced suspended solids (Zhang et al., 2016). The model results of the vertical structure of currents suggested that in Sungo Bay, suspended aquaculture (kelp and bivalves) reduced average flow velocity by 40–54% (Grant and Bacher, 2001; Shi et al., 2011). We inferred that the strong attenuation of flow and turbulence in KF effectively reduced sediment resuspension and suspended solids,

thus improving water clarity, although our study did not measure flow velocity in situ.

4.2. Alleviation of eutrophication and acidification by kelp farming

Seaweed cultivation has been widely proposed as a biofilter to absorb dissolved nutrients and alleviate eutrophication in coastal waters (Buschmann et al., 2001, 2017; Chung et al., 2002; Neori et al., 2004; Yang et al., 2015a; Segheta et al., 2016; Xiao et al., 2017). Among different seaweeds, *S. japonica* exhibited high nutrient uptake under laboratory conditions (Xu et al., 2011). Table 1 shows that kelp farming reduced DIN by 5.8% and DIP by 2.5%. This removal efficiency of nutrients in XSB was considerably lower than the efficiencies of those cultivated by *Porphyra yezoensis* along the Lusi coast (He et al., 2008), by *Gracilaria verrucosa* in Hangzhou Bay (Huo et al., 2011), and by *G. lemaneiformis* near the Nan'ao Island (Huang et al., 2017). He et al.

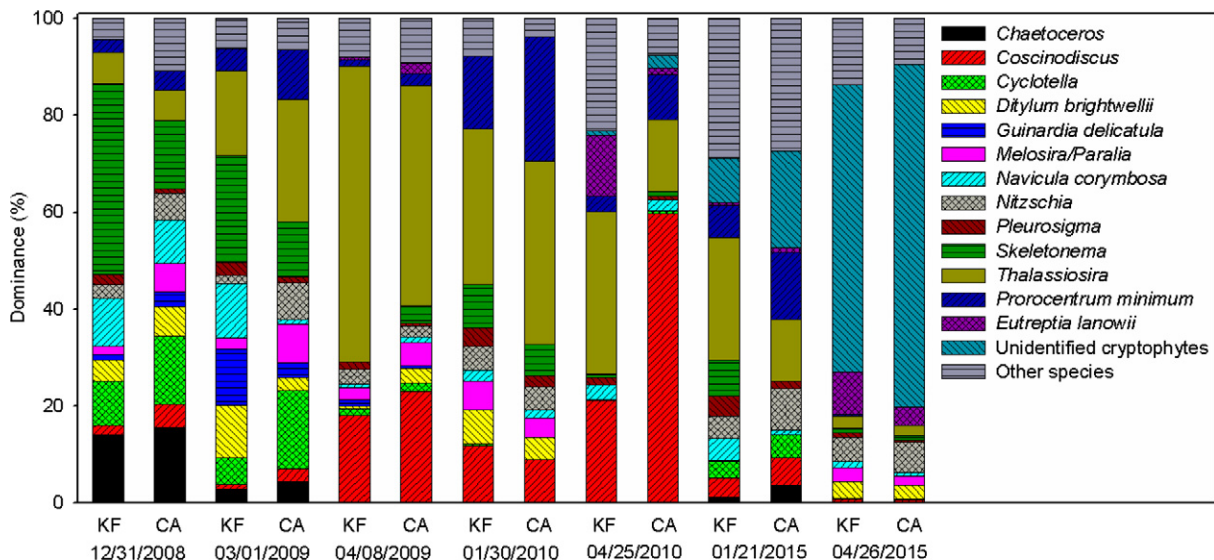


Fig. 5. Dominant species/genera in the kelp farm (KF) and control area (CA) during the kelp culture period.

Table 2

Results (*R* value) of two-way analysis of similarity (ANOSIM) for phytoplankton community between regions and water layers on different dates. KF: kelp farm; CA: control area. ^{ns}No significance; **p* < 0.05; ***p* < 0.01. Superscripted lower-case letters of different dates indicate presence/absence of the kelp cultivation. ^a: during the kelp culture period; ^b: after the kelp harvesting.

Date	KF vs. CA	Surface vs. bottom
12/31/2008 ^a	0.679 ^{***}	0.122 ^{ns}
03/01/2009 ^a	0.998 ^{***}	0.637 ^{***}
04/08/2009 ^a	0.960 ^{***}	0.288 [*]
01/30/2010 ^a	0.806 ^{**}	0.400 [*]
04/25/2010 ^a	0.963 ^{***}	0.551 ^{**}
01/21/2015 ^a	0.380 ^{**}	-0.081 ^{ns}
04/26/2015 ^a	0.574 ^{***}	0.628 ^{**}
05/21/2009 ^b	0.062 ^{ns}	0.333 [*]
08/05/2009 ^b	-0.241 ^{ns}	0.519 [*]
07/14/2010 ^b	-0.037 ^{ns}	0.444 [*]
11/17/2010 ^b	-0.259 ^{ns}	-0.204 ^{ns}
07/18/2015 ^b	0.157 ^{ns}	0.143 ^{ns}
10/15/2015 ^b	0.037 ^{ns}	0.096 ^{ns}

(2008) observed that *Porphyra* farming resulted in the reduction of NH₄, NO₂, NO₃, and DIP by 50–94%, 42–91%, 21–38%, and 42–67%, respectively. By contrast, Huang et al. (2017) found that *G. lemaneiformis* farming reduced DIN and DIP by 7.4% and 15%, respectively. This difference is attributable to differences in cultivation area and background nutrient levels. The old (~20–50 ha) and new (~200 ha) KF areas in our study were much smaller than that (300 ha) of the *Porphyra* farm (He et al., 2008). In addition, average concentrations of DIN (51.34 μmol/L) and DIP (2.22 μmol/L) in the middle XSB and Xihu Harbor were considerably higher than those (DIN and DIP at 13.03 and 0.40 μmol/L, respectively) near the Nan'ao Island (Huang et al., 2017). Nutrient deficits in the present study are also attributable to the surplus phytoplankton biomass in KF (Fig. 3), which absorbed partial nutrients and contributed to nutrient removal. For example, DSI in KF was reduced by 2.2% through phytoplankton consumption (Fig. 2i).

Assuming the average N (3.71%) and P (0.52%) contents in kelp tissue by dry weight compiled by Xiao et al. (2017), the present kelp harvest (with an annual production of 8000 t by dry weight) will remove, annually, 297 t of N and 42 t of P from XSB. Xiao et al. (2017) estimated that seaweed cultivation in China removed 75,000 t of N and 9500 t of P annually. To reduce nutrient discharge from fish aquaculture, the cage-culture area in XSB decreased from 2500 ha (Huang et al., 2008) in 2000 to 55.7 ha in 2016, according to our unpublished remote-sensing data. Due to lack of the present fish production data, we estimated an annual production (299.1 t) of cage-culture fish in 2016 based on the reported annual production (13,422.6 t) in 2000 (Huang et al., 2008). Assuming an annual input of N (958.38 t) and P (142.38 t) into XSB from fish cages (Huang et al., 2008), the present annual N and P discharged from fish cages were roughly estimated to be 21.36 and 3.17 t, respectively. These values were considerably lower than those of the removal of N and P by kelp farming, suggesting that kelp cultivation efficiently absorbs nutrients from fish cages and is useful in the bioremediation of eutrophication. In previous decades, the application of seaweeds to integrated multi-trophic (e.g., bivalves and fish) aquaculture has been adopted worldwide, particularly in China (Troell et al., 1997; Chopin et al., 2001; Neori et al., 2004; Mao et al., 2009; Marinho-Soriano et al., 2009; Yang et al., 2015a; Buschmann et al., 2017). Other field investigations in XSB have also discovered that *Gracilaria* is efficient in removing DIN and DIP, particularly in summer (Jiang et al., 2010; Huo et al., 2012). To balance the DIN absorbed by seaweed and discharged by fish cages, Jiang et al. (2010) suggested that the optimal co-cultivation proportion of fish (*Lateolabrax japonicus* and *P. crocea*) cages to *Saccharina* and *Gracilaria* was 1 cage to 450 m² and 1 cage to 690 m², respectively. Subsequently, Huo et al. (2012) estimated that the optimal co-cultivation proportion of *P. crocea* to *G. verrucosa* was 1 cage to 145 m² or 1 kg to 7.27 kg. Nevertheless, the present removal of N and P from kelp farming

is of an order of magnitude lower than that from terrigenous input (Huang et al., 2008).

In addition to the bioremediation of eutrophication, kelp farming slightly increased DO and pH (Fig. 2; Table 1). This finding is consistent with other reports in the mesocosms (Yang et al., 2015a) and field (Huang et al., 2017; Xie et al., 2017; Liu et al., 2019). For example, Liu et al. (2019) found significantly higher pH and DO in a *Gracilaria* farm than in its CA and fish-cage area. Seaweeds effectively sequester carbon dioxide (CO₂) and release O₂ during photosynthesis, resulting in increases in pH and DO in the cultivated farm. According to annual kelp productions in XSB and China, as well as the carbon (25–31%) content in kelp tissue (Yang et al., 2015a), we estimated that kelp cultivation will annually remove 2000–2480 t of C from XSB and 585,968–726,600 t of C from China's coastal waters. Therefore, large-scale seaweed cultivation is a potentially sink for CO₂ and has a potential to alleviate coastal acidification (Chung et al., 2013; Tang et al., 2011; Yang et al., 2015a).

4.3. Enhancement of phytoplankton biomass and diversity by kelp farming

Our study demonstrated that kelp farming appreciably increased phytoplankton biomass (Fig. 3; Table 1). Earlier studies have suggested that phytoplankton biomass in XSB was largely limited by light penetration and water column stability rather than by nutrients (Jiang et al., 2019b, 2019c). As mentioned, kelp farming greatly reduced flow velocity, turbulence, and suspended solids and increased transparency (Fig. 2; Table 1), thus improving water clarity and enhancing water column stability. These physical changes markedly mitigated the severe light limitation on phytoplankton and stimulated phytoplankton growth in KF, resulting in a higher phytoplankton biomass in KF than in CA.

Our finding is inconsistent with other observations in macroalgal farms (Huo et al., 2011; Yang et al., 2015a; Huang et al., 2017; Zhang et al., 2018) and mesocosm experiments (Yang et al., 2015a, 2015b). Laboratory experiments have demonstrated that seaweeds significantly inhibit phytoplankton photosynthesis and growth via allelopathy (Nan et al., 2004; Tang and Gobler, 2011; Han et al., 2013; Ye et al., 2014; Tang et al., 2015; Yang et al., 2015b). We deduced that increase/decrease in the phytoplankton biomass of a macroalgal farm is largely determined by local physicochemical properties, especially that of nutrients and light penetration. For example, concentrations of nutrients (particularly DIP) and suspended solids were considerably lower around Nan'ao Island (Huang et al., 2017; Zhang et al., 2018) than in XSB (Fig. 2e; Jiang et al., 2019b), suggesting that phytoplankton growth in the *Gracilaria* farm was largely limited by nutrients rather than by water clarity. Therefore, the phytoplankton biomass decreased in the *Gracilaria* farm near Nan'ao Island via nutrient competition and allelopathy (Yang et al., 2015a; Huang et al., 2017; Zhang et al., 2018). The increased phytoplankton biomass in KF is also attributable to the relatively low allelopathy and nutrient competition therein. DIN (51.34 μmol/L) and DIP (2.22 μmol/L) in XSB are abundant enough to support phytoplankton growth and thereby weaken allelopathy and nutrient competition between the kelp and phytoplankton. We hypothesize that phytoplankton growth in macroalgal farm in turbid, highly eutrophic waters was largely regulated by flow attenuation and improvements in light penetration rather than allelopathic effects and resource competition.

Our study demonstrated that kelp farming greatly enhanced phytoplankton diversity (Fig. 4; Table 1). This finding is consistent with previous reports from microscopic (Huo et al., 2011; Jiang et al., 2012) and metagenomic (Chai et al., 2018) examinations. Similarly, *Gracilaria* farming was observed to increase planktonic microbial diversity (Xie et al., 2017). KF provides diverse microhabitats (e.g., phycosphere, shading, and those from environmental heterogeneity), which favors the occurrence and growth of various phytoplankton species. Additionally, we found numerous epiphytic diatoms (e.g., *Navicula*, *Pleurosigma*, *Gyrosigma*, and *Diploneis*) that were shed from the kelp thalli, resulting

in increased species diversity. Our previous study observed significantly increased phytoplankton *S* in oyster farms due to divorced epiphytic/epizoic diatoms (Jiang et al., 2019a). Earlier studies have also observed that *Gracilaria* farming inhibited phytoplankton bloom via allelopathic effects (Huo et al., 2011; Chai et al., 2018; Yang et al., 2015a), which enhanced species diversity. Furthermore, the specificity of phytoplankton species response to macroalgal allelopathy has been widely recognized (Jeong et al., 2000; Nan et al., 2004; Tang and Gobler, 2011; Han et al., 2013; Tang et al., 2015; Yang et al., 2015b). We inferred that the diverse microhabitats and allelopathy in KF contributed to enhanced phytoplankton diversity, which strengthens the stability of the phytoplankton community and the functioning of the ecosystem (Ptacnik et al., 2008).

4.4. Reorganization of phytoplankton community composition by kelp farming

Phytoplankton community composition differed significantly ($p < 0.01$) between KF and CA (Table 2). This, according to SIMPER results, was largely attributed to the different responses of various phytoplankton species (large- vs. small-celled, colonial vs. single-celled, planktonic vs. benthic or epiphytic, and high- vs. low-silicious) to kelp farming (Table S5). However, no significant difference was found in the phytoplankton size structure (Table S3). Phytoplankton community composition in XSB varies significantly under physical gradients (e.g., water column stability, sedimentation, and light), in addition to nutrients, due to their physiological and ecological trade-offs (Jiang et al., 2019c). Fig. 5 confirms that the dominances of long-chained planktonic (*Skeletonema*, *Thalassiosira*, and *G. delicatula*) and epiphytic (*N. corymbosa* and *Pleurosigma*) diatoms were usually higher in KF than in CA, whereas the dominances of benthic (*Nitzschia* and *Melosira/Paralia*) and large-celled planktonic (*Coscinodiscus* and *Cyclotella*) diatoms and small single-celled species (*P. minimum* and cryptophytes) were lower in KF than in CA. This finding suggested that the dominant species/genera were highly correlated with the physical changes caused by kelp farming. For example, the reduction in flow and turbulence in KF resulted in stronger sedimentation (sinking loss) of heavy, high-silicious, benthic diatoms and large-celled planktonic diatoms with lower buoyancy than that of light, low-silicious, and long-chained planktonic diatoms with higher buoyancy (Pančić and

Kjørboe, 2018). Our earlier study in XSB affirmed that planktonic colonial diatoms thrive in stable, high-transparency waters, whereas large, single-celled planktonic diatoms and benthic diatoms are dominant in turbulent, turbid waters (Jiang et al., 2019c). Additionally, epiphytic diatoms may be divorced from the kelp thallus as well as rafts and their associated biofouling assemblages, resulting in higher dominances of *N. corymbosa* and *Pleurosigma* in KF than in CA (Fig. 5). Huo et al. (2011) found that the dominance of *Pleurosigma* was much higher in the *Gracilaria* farm than in CA, and vice versa for benthic diatom *M. moniformis*. However, *Gracilaria* farming increased *Chaetoceros* dominance but reduced *Skeletonema* dominance. This result is inconsistent with our finding, which warrants further investigation. Xie et al. (2017) demonstrated that planktonic microbial community differed significantly between the *Gracilaria* farm and CA because of physico-chemical changes and seaweed processes. These results confirmed our hypothesis that kelp cultivation significantly shapes phytoplankton community composition.

4.5. Implication and suggestion

The present study demonstrated that kelp cultivation effectively improved water quality and enhanced phytoplankton diversity. We have established a conceptual model to summarize how kelp farming influences the water quality and phytoplankton community (Fig. 6). To effectively alleviate eutrophication, remedy acidification (increased CO₂ sequestration), enhance biodiversity, and control HABs, we proposed to expand the cultivation scale of economic seaweeds in coastal eutrophic waters. Notably, temperate-adapted (e.g., *Saccharina* and *Porphyra*) and warm-adapted (e.g., *Gracilaria/Gracilariopsis* and *Sargassum*) macroalgae should be cultivated alternately in cold and warm seasons in subtropical waters to overcome the adverse effects of seasonal temperature variations on macroalgal growth and production. Because seaweed diversity enhances nutrient uptake (Bracken and Stachowicz, 2006), co-culture of different seaweed species have also been proposed to increase the bioremediation efficiency of eutrophication (Buschmann et al., 2008).

However, our study indicated that kelp farming increased phytoplankton biomass under reductions in light limitation and high concentrations of background nutrients (Fig. 6). To reduce phytoplankton

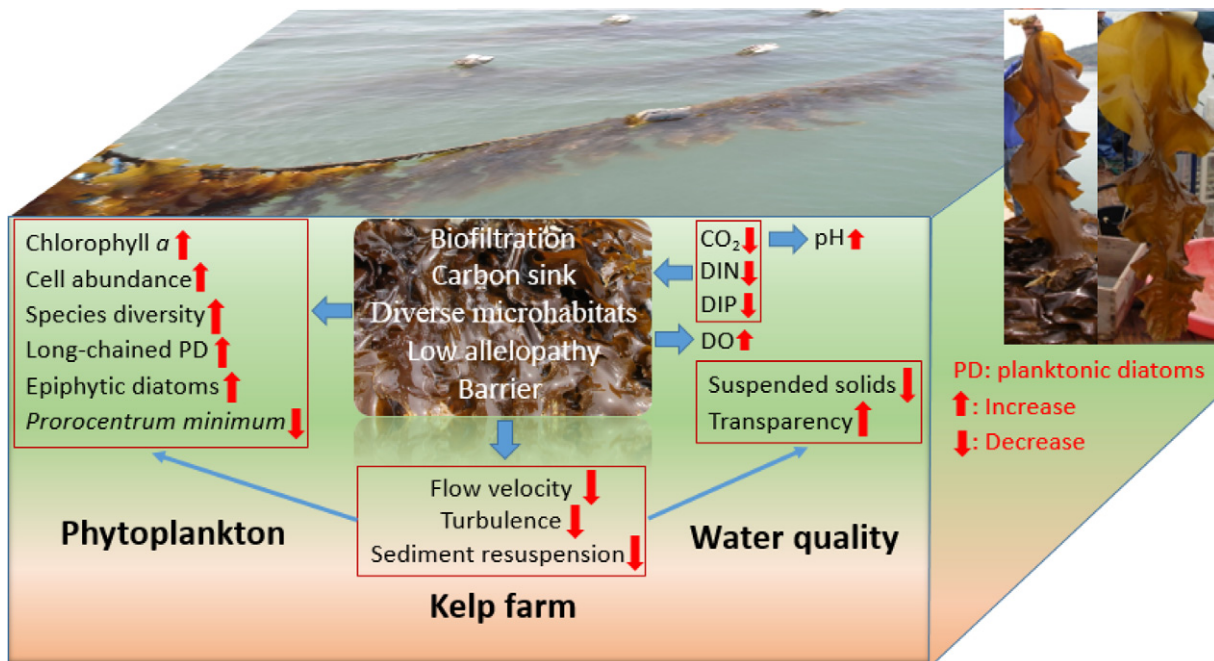


Fig. 6. A conceptual model for summarizing the influence of kelp farming on water quality and phytoplankton community in Xiangshan Bay.

biomass and algal blooms and enhance water clarity, we proposed to cultivate bivalves (e.g., oyster and scallop) integrated with seaweeds in turbid, eutrophic waters. Our previous work in XSB has demonstrated that oyster farming greatly reduced phytoplankton biomass and water turbidity and effectively alleviated algal blooms and eutrophication (Jiang et al., 2019a). Shellfish filters and consumes phytoplankton and particulate organic matter, which incorporated nutrients and carbon into shellfish tissues and shell (Tang et al., 2011; Rose et al., 2014; Jiang et al., 2019a). Additionally, the shellfish harvesting represents a net removal of nutrients and carbon from the ecosystem. Due to bioextraction of nutrients and filtration of phytoplankton, shellfish aquaculture has been strongly proposed during coastal nutrient management (Rose et al., 2014; Bricker et al., 2018; Jiang et al., 2019a). Therefore, aquaculture/remediation of seaweeds and bivalves has the potential to alleviate eutrophication, acidification, and HABs in China coastal waters. Further studies are warranted on marine spatial planning of integrated multi-trophic aquaculture (e.g., seaweeds and bivalves) and ecological restoration in local eutrophic systems, although their application to integrated multi-trophic aquaculture has been widely adopted (Chopin et al., 2001; Neori et al., 2004; Mao et al., 2009; Rose et al., 2014). For ecosystem-based marine spatial planning purposes, high spatial resolution predictive model, including ecosystem-scale and local-scale approaches, are needed (Filgueira et al., 2014; Bagdanavičiūtė et al., 2018; Bricker et al., 2018; Zhang and Thomsen, 2019).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We are grateful to Xiaoya Liu and Huaguo Zhang for providing physicochemical and remote-sensing data. This work was supported by the National Key Research and Development Program of China (2018YFD0900901), Scientific Research Fund of the Second Institute of Oceanography, Ministry of Natural Resources (QNYC1703 and JT1602), National Natural Science Foundation of China (41876198 and 41776119), National Marine Public Welfare Research Project of China (201305043-3), Project of State Key Laboratory of Satellite Ocean Environment Dynamics, Second Institute of Oceanography (SOEDZZ1803), and Project of Long-term Observation and Research Plan in the Changjiang Estuary and Adjacent East China Sea (LORCE).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.135561>.

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