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Dissolved organic carbon from cultured kelp *Saccharina japonica*: production, bioavailability, and bacterial degradation rates

Yaping Gao[1,2], Yitao Zhang[3], Meirong Du[1,2], Fan Lin[1,2], Weiwei Jiang[1,2], Wenhao Li[4], Fengxue Li[1], Xuning Lv[5], Jinghui Fang[1,2], Zengjie Jiang[1,2,*]

[1]Yellow Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Qingdao 266071, PR China
[2]Laboratory for Marine Fisheries Science and Food Production Processes, Pilot National Laboratory for Marine Science and Technology (Qingdao), Qingdao 266237, PR China
[3]Chudao Aquatic Products Co. Ltd., Rongcheng 264312, PR China
[4]Shanghai Ocean University, Shanghai 201306, PR China
[5]University of Chinese Academy of Sciences, Beijing 100049, PR China

ABSTRACT: Seaweed farming is widely perceived as one of the most environmentally benign types of aquaculture activity. In the past 10 yr, global seaweed production has doubled and reached 31.8 million t. Farmed seaweed also has important functions in local ecosystems. We focus on the production, bioavailability, and bacterial degradation rates of dissolved organic carbon (DOC) from cultured kelp *Saccharina japonica*. Semi *in situ* incubations in 2 growing seasons were conducted to estimate DOC production, and laboratory incubations were used to determine bioavailability and decay rates of DOC from cultured kelp. Results showed that DOC production was 6.2–7.0 mg C (g dry wt)$^{-1}$ d^{-1} in the growing seasons, and the proportion of DOC in net primary production was 23.7–39.1%. The decomposition rate of DOC was 4 ± 1% d^{-1} and 9 ± 1% d^{-1} in January and April, respectively. About 37.8% remained as refractory DOC after 150 d incubation. It was calculated that the total DOC from kelp in Sanggou Bay was approximately 11.3 times of that from phytoplankton for the whole bay (144 km^2). Our results suggest that more than half of the bioavailable DOC will be exported out of the bay to potentially support the wider food chain through bacterial uptake. Cultured kelp is therefore an important source of DOC in the embayment, contributes to the coastal DOC pool and provides a potential pathway for carbon dioxide sequestration.

KEY WORDS: Cultured kelp · *Saccharina japonica* · Bioavailability · Degradation rates · DOC productivity · Export

1. INTRODUCTION

Marine dissolved organic carbon (DOC) represents one of the largest and most exchangeable organic carbon pools on Earth and plays an important role in marine biogeochemical cycles. In addition to the well-recognized phytoplankton, macroalgae are also major primary producers contributing to marine newly synthesized DOC (Khailov & Burlakova 1969, Sieburth 1969, Søndergaard 1981). The ecological role of DOC in coastal ecosystems depends on its decomposition process. Within a particular ecosystem, some of the DOC can be degraded within the system (Lønborg et al. 2009, Lønborg & Álvarez-Salgado 2012), rapidly utilized through biological uptake as bioavailable DOC (BDOC), remineralized

*Corresponding author: jiangzj@ysfri.ac.cn

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to inorganic constituents (Ducklow et al. 1986), and reincorporated via microbial organisms (i.e. in the microbial loop, Azam et al. 1983) to higher trophic levels. On the other hand, a large proportion of the DOC will be exported out of the system to the open sea to degrade or be transformed into refractory dissolved DOC (RDOC) (Ogawa et al. 2001, del Giorgio & Duarte 2002, Jiao et al. 2010, Lechtenfeld et al. 2015) and thus potentially contribute to global carbon sequestration (Krause-Jensen & Duarte 2016).

Quantitative evaluation of DOC production by seaweeds depends on DOC absolute release rate and the fraction of DOC in net primary production (NPP). Laminarian brown macroalgae (kelp) release 13–62% of their photosynthetic captured carbon as DOC (Khailov & Burlakova 1969, Abdullah & Fredriksen 2004, Wada et al. 2007, Reed et al. 2015). The released DOC contributes to the coastal DOC pool. In some coastal environments, macroalgal DOC contribution can reach 20% of the total DOC concentrations (Wada et al. 2007, Wada & Hama 2013). It has been shown that about 53.7% of released DOC is mineralized in 30 d decomposition experiments (Wada et al. 2008), and that DOC from kelp is more refractory than DOC from phytoplankton, which can be removed by bacteria in days to weeks (Kirchman et al. 1991, Chen & Wangersky 1996, Hama et al. 2004, Davis & Benner 2007), because bioavailability of DOC varies depending on DOC chemical composition (Benner & Opsahl 2001, Wada et al. 2007) and production of refractory components (Cottrell & Kirchman 2000, Lønborg et al. 2009). Data on mineralization of DOC at a longer time scale is limited. Most of the incubations lasted a few days to 2 mo (Wada et al. 2008), and the remaining refractory DOC fraction was unclear. In a particular coastal ecosystem, the DOC fate (utilization versus export) and its function in the local system will depend on the balance between the half-life of DOC and the water residence time (Lønborg & Álvarez-Salgado 2012).

Seaweed culture is a rapidly developing industry and plays an important role in the supply of seafood and raw industrial materials. It is widely perceived as one of the most environmentally benign types of aquaculture. In 2016, global production of algae reached 31.8 million t (FAO 2018). In aquaculture ecosystems, the effects of macroalgae on dissolved inorganic nutrient cycles (i.e. inorganic carbon, nitrogen, phosphorus, and silicates) have received more attention (Jiang et al. 2013, Li et al. 2016, Ning et al. 2016), while DOC has not been well studied (Mahmood et al. 2017, Wang et al. 2017).

The production of macoroalgae in China accounts for 48.6% of the global supply (FAO 2018). Among the species cultured in China, the kelp *Saccharina japonica* is the most important. In natural kelp populations, the production of DOC shows high variability (Khailov & Burlakova 1969, Sieburth 1969, Abdullah & Fredriksen 2004, Reed et al. 2015). Research on DOC production in cultured kelp is limited; the bioavailability of kelp DOC remains unclear, and the function of DOC in culture systems has not been evaluated to date.

Sanggou Bay is the largest kelp culture region in north China, with a culture area of 83 km^2 and production of up to 79 000 t in dry weight (Rongcheng Fisheries Technology Extension Station 2017). Kelp thallus OC is removed from the ecosystem when harvested, while DOC is released into the embayment throughout the whole period of growth. In this study, we performed (1) semi-*in situ* incubation to estimate DOC production by cultured *S. japonica*, (2) laboratory incubation to determine the bioavailability and decay rates of DOC, and (3) analysis to provide an assessment of cultured kelp as a net source of DOC that helps fuel the microbial foodweb in the nearshore water column.

2. MATERIALS AND METHODS

2.1. Study site

Sanggou Bay is a temperate semi-enclosed bay at the eastern end of the Shandong Peninsula in China (122° 24′ – 122° 35′ E, 37° 01′ – 37° 09′ N). The north, west, and south sides of the bay are surrounded by land, and the mouth opens into the Yellow Sea (Fig. 1). The bay is approximately 11.5 km in length and 7.5 km in width from east to west, with an area of 144 km^2. The average water depth is 7.5 m and the maximum offshore water depth reaches 33 m. The seasonal variation in water temperature in the bay is 1.8–26.2°C, and salinity is 29.1–31.8 psu (Zhu et al. 2017). Kelp is the most important aquaculture species in the bay and typically cultivated from November to the following May to July using the suspended longline method.

2.2. Incubation and sampling method

We performed incubations in Sanggou Bay in late January and late April, representing the winter and spring farming seasons, respectively. An outdoor semi-*in situ* culture system was established in the dock and used for the incubations (Fig. 2). In this

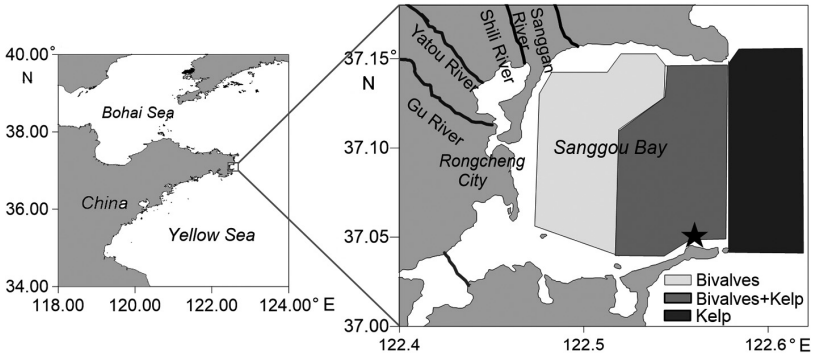

Fig. 1. Sanggou Bay, China, showing the culture areas and the incubation experiment site (★)

system, 125 l cylindrical acrylic containers (40 cm in diameter and 100 cm in height) were placed in a large storage tank (4 m × 3 m × 0.9 m) into which seawater was continually pumped (40 m^3 h^{-1}) to maintain a water temperature similar to that of the kelp's natural environment. Kelps were collected from longline culture ropes in Sanggou Bay and transported to the storage tank in water within 15 min.

A single plant was introduced into each of the 6 cylinder containers (n = 6), while 3 containers without kelp served as controls (n = 3). Submersible pumps were placed on the side wall of each container to simulate the hydrodynamic conditions in a natural culture environment (with velocities of approximately 0.06 m s^{-1}, measured by JFE Advantech Model AEM - USB current meters hung in the container). Kelps were hung in the tops of the containers in the same manner as in the longline culture (Fig. 2). Due to the short time out of water during collection, kelps were acclimated for 1 day in the containers in flowing water. Then seawater was changed and incubation experiments began. Silicon rubbers were used to plug the openings in the cylinder container. The incubation lasted for 25 h, to cover the whole tidal cycle.

During the incubation, oxygen and temperature in each container were measured using a dissolved oxygen portable meter (Orion3-star, Thermo Electron) every 2 h during the day and 6 h during the night (smaller change during the night than the day) to evaluate NPP and respiration (*R*). All of the 6 replicate containers were used to calculate the NPP and *R*. Light intensity of the surface water (at a depth about 0.5–1 cm) in a randomly selected control container was recorded continuously by a PAR logger (DEFI2-L, JFE Advantec). The light vertical attenuation coefficient (*K*) in control containers (n = 3) was calculated from the slope of the linear regression of the natural logarithm of PAR. versus depth.

Three replicate 30 ml samples were extracted by glass pipette from each container at the beginning and end of the incubation for evaluation of DOC concentration. After filtering through 0.7 µm Whatman GF/F glass fibre filters, the water was stored in glass bottles and sealed in bubble-free states. Then the water samples were placed on ice and transported to the laboratory. The pipettes, glass bottles and GF/F filters that had been previously used were all pre-combusted (450°C, 5 h).

The water volume of each container and the mass (wet weight and dry weight) and length of each kelp was determined at the end of the incubation and used to determine the primary production and DOC production for each kelp plant. Triplicate water samples in each container were filtered through a 0.45 µm Millipore cellulose membrane filter and transported to the laboratory for inorganic nutrient analyses. Nitrate (NO_3^-) and ammonium (NH_4^+) were analyzed using the standard pink azo-dye and phenol hypochlorite-indophenol blue method methods, respectively. Phosphate (PO_4^-) was determined using the molybdenum-blue method. All of the above dissolved inorganic nutrient analyses followed the methods of Parsons et al. (1984).

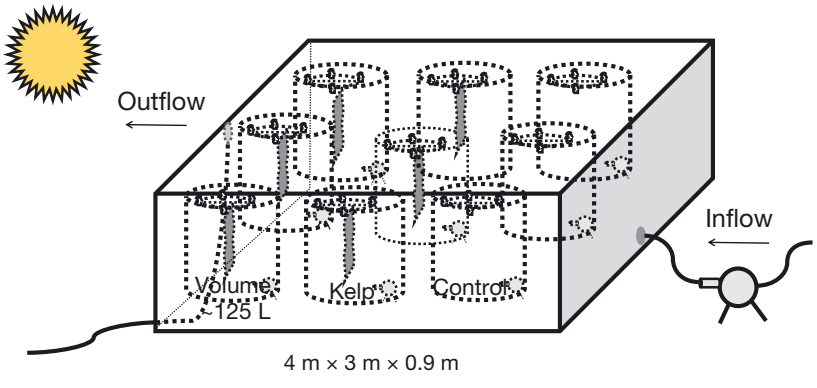

Fig. 2. Schematic diagram of the incubation experiment system. The cylinder containers (40 cm in diameter and 100 cm in height) were placed in a large storage tank into which seawater was continually pumped to maintain a water temperature similar to that of natural seawater. Submersible pumps were placed on the side wall of cylinder to simulate the hydrodynamic conditions in the field

Three replicates of 2 l water were also sampled for each cylinder container for the biodegradation experiment. In the laboratory, 1.5 l water samples were filtered through 0.7 µm GF/F filters and transferred to 2 l amber glass bottles. Then, 75 ml water samples were filtered through 1.2 µm GF/C filters and added as inoculum to the 1.5 l water to establish amicrobial culture (Lønborg et al. 2009). The use of GF/C filters allowed for the passage of both autotrophic and heterotrophic microorganisms that were <1.2 µm, while autotrophic growth was prevented during the incubation in the dark. The experiments were conducted in the dark over a period of 150 d at 4°C and 14°C for the January and April samples, respectively. This time scale allows the decay of both the labile and semi-labile parts of the DOC pool. Samples of 30 ml of water were taken at Days 0, 5, 15, 30, 60, 90, and 150 and analyzed immediately after sampling.

2.3. Analytical methods, calculations and statistical analyses

NPP and *R* in the 6 containers were estimated using changes in dissolved oxygen concentration in each container, based on the difference in O_2 concentration during the time samples spent in illumination and the dark, respectively. Gross primary production (GPP) was calculated as the sum of NPP and *R*. Oxygen evolution rates were converted to carbon using a photosynthetic quotient of 1 (Rosenberg et al. 1995). Primary production and respiration for each plant were normalized by their dry weight.

The difference in DOC between the beginning and end of the incubation period (water was not changed during the incubation) in each control container was considered as the DOC production by phytoplankton or consumption by planktonic microbes The DOC value in the controls was subtracted from the value in kelp containers to yield the DOC production of kelp. DOC concentration in the filtered water samples was measured using the high-temperature catalytic oxidation (HTCO) technique using a CN analyzer (TOC-VCPH, Shimadzu) (water samples were fed directly and analyzed).

The kinetics of DOC degradation were described by a first-order exponential decay model with the refractory pool taken into account:

$$\mathrm{DOC}(t) = \mathrm{BDOC} \cdot \exp\left(-k_{\mathrm{DOC}} \cdot t\right) + \mathrm{DOC}\,(150) \quad (1)$$

where DOC(*t*) is the amount of DOC remaining at time *t* for the control and kelp treatments. The control measures are subtracted from the kelp measures at each time *t* to prevent microorganism sources of DOC from being considered as kelp sources. BDOC (in mg l^{-1}) is the degraded DOC during the 150 d period, k_{DOC} the degradation rate constant, calculated by the fitting the decay model (in d^{-1}), *t* is time (d), and DOC(150) (in mg l^{-1}) is the remaining RDOC pool after 150 d of incubation.

A *t*-test was used to detect if NPP, GPP, *R* and DOC production rate were different between the 2 months using SPSS 17.0. The significance level was set at 0.05 for all tests.

3. RESULTS

Temperature ranged from −1.3 to 1.7°C during the January incubation and 14.7 to 17.8°C in April (Table 1). Surface PAR for the January incubations was 0–1482 µmol m^{-2} s^{-1} with the PAR diffuse attenuation coefficient (K) = 2.18. In April the surface light were 0–1928 µmol m^{-2} s^{-1} and K was 1.47. During 24 h incubations, 19.2, 30.0, and 13.9% of NO_3^-, NH_4^+ and PO_4^-, respectively, were absorbed in January and 54.1, 69.5, and 27.3% in April.

Table 1. Kelp and water parameters in the incubation containers. Data are mean ± SE (where applicable)

	January	April
Kelp dry weight (end of incubation, g)	7.23 ± 2.15	39.3 ± 9.15
Kelp wet weight (g)	103.1 ± 24.2	316.5 ± 53.3
Kelp length (cm)	73.6 ± 6.6	129.6 ± 20.4
Temperature (°C)	−1.3 to 1.7	14.7 to 17.8
Surface irradiance (µmol m^{-2} s^{-1})	0 to 1482	0 to 1928
PAR attenuation coefficient K	2.18 ± 0.17	1.47 ± 0.37
NO_3^- (average initial to end, µmol l^{-1})	8.4 ± 0.3 to 6.8 ± 1.2	7.4 ± 0.6 to 3.4 ± 0.9
NH_4^+ (µmol l^{-1})	2.4 ± 0.04 to 1.69 ± 0.69	2.6 ± 0.1 to 0.8 ± 0.4
PO_4^- (µmol l^{-1})	0.36 ± 0.02 to 0.31 ± 0.04	0.33 ± 0.01 to 0.24 ± 0.05
DOC (mg l^{-1})	3.5 ± 0.05 to 3.92 ± 0.97	3.9 ± 0.11 to 5.7 ± 1.6

The NPP of kelp in January was 29.7 mg C (g dry wt)$^{-1}$ d^{-1} (Fig. 3), which was significantly higher than the 15.9 mg C (g dry wt)$^{-1}$ d^{-1} in April ($p < 0.05$). *R* was 4.3 mg C (g dry wt)$^{-1}$ d^{-1} in January, while in April the respiration reached 10.7 mg C (g dry wt)$^{-1}$ d^{-1}. GPP was 34.0 and 26.7 mg C (g dry wt)$^{-1}$ d^{-1} in January and April, respectively (Fig. 3).

The DOC production rate was 7.0 mg C (g dry wt) $^{-1}$ d^{-1} in January and 6.24 mg C (g dry wt)$^{-1}$ d^{-1} in April (Fig. 4). The proportion of DOC to NPP was 23.7 and 39.1% in January and April, respectively, with a mean value of 31.4%. No significant difference was found between the 2 incubations for both the DOC production rate and DOC to NPP ($p > 0.05$).

The incubation for the degradation of kelp DOC showed that BDOC production was 4.23 mg C (g dry wt) $^{-1}$ d^{-1} in January and 3.83 mg C (g dry wt) $^{-1}$ d^{-1} in April (Fig. 5). After the 150 d decay, 37.3 and 38.2% were left as RDOC for the January and April incubation, respectively. No significant difference was detected for the DOC release rate and bioavailability and refractory DOC production rate ($p > 0.05$). The decomposition rate from the first-order exponential decay model showed that DOC was degraded at a rate of 4 ± 1% d^{-1} and 9 ± 1% d^{-1} in the January and April incubation, respectively (Fig. 6), and the corresponding half-life times of BDOC ($\ln 2/k_{DOC}$) were 15.8 d and 5.3 d, respectively.

The water residence time in Sanggou Bay is about 16.6 d in the middle part, 2.1–8.3 d in the outer kelp culture area, and <2.1 d in the outer area of the bay (Shi & Wei 2009). Kelp culture is mainly in the outer area of the bay (Fig. 1). Therefore, calculated using the range of values of 2.1 to 8.3 d, 8.8–30.6% and 23.9–66.0% of BDOC will be mineralized in the system in January and April, respectively, while

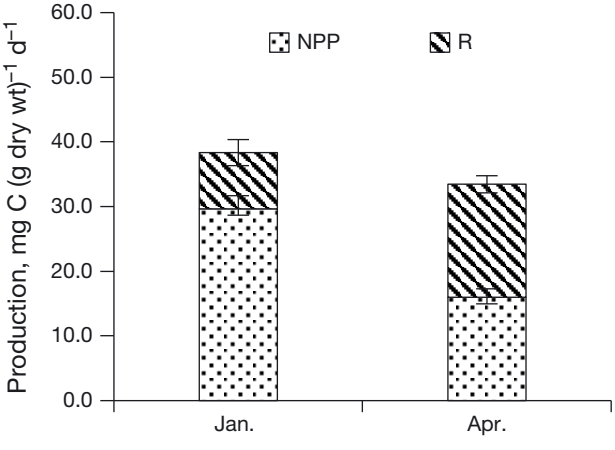

Fig. 3. Primary production of kelp in the January and April incubations. Data are mean ± SD, n = 6

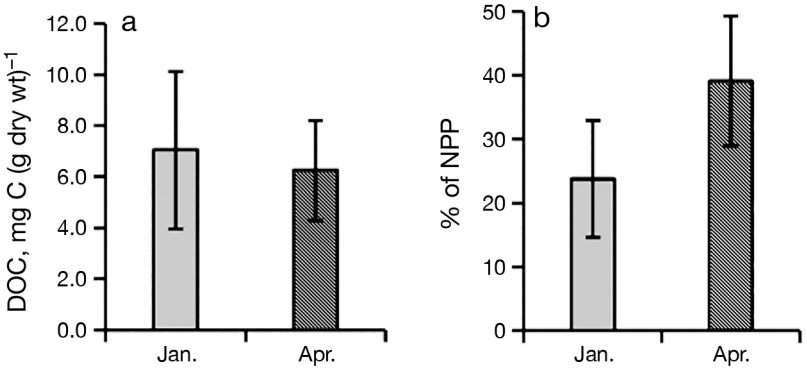

Fig. 4. (a) Dissolved organic carbon (DOC) production rate and (b) DOC percent of NPP in January and April incubations. Data are mean ± SD, n = 6

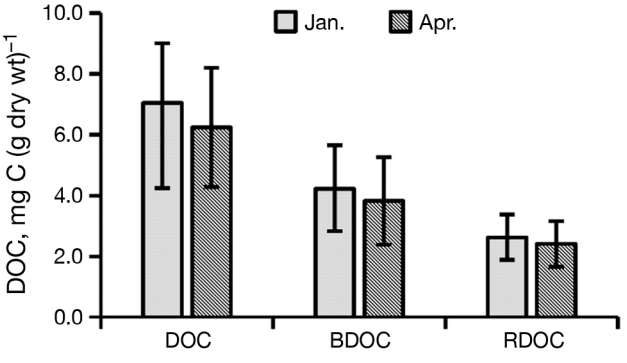

Fig. 5. Total DOC, bioavailable dissolved organic carbon (BDOC), and refractory dissolved organic carbon (RDOC) in the January and April incubations. Data are mean ± SD, n = 6

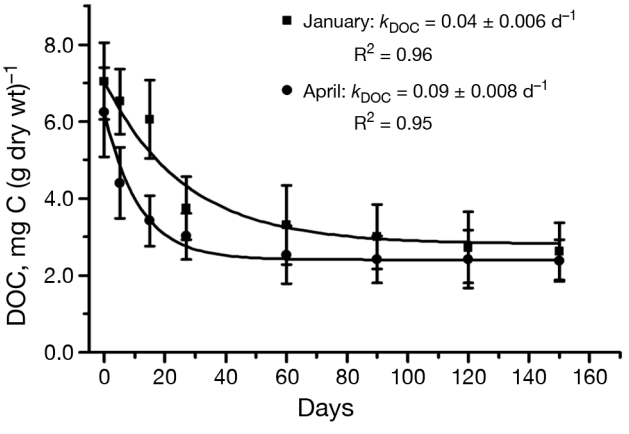

Fig. 6. Decay of bioavailable dissolved organic carbon (BDOC) from sample water collected during the January and April incubations. The solid line represents the predictions of the exponential decay model, values are mean ± SD, n = 6

69.4–91.2% and 34.0–76.1% will be exported out of the bay, respectively, entering the Yellow Sea, where no kelp is cultured and phytoplankton is the main primary producer.

4. DISCUSSION

Both the absolute release rate of DOC and the proportion of DOC in NPP are important in evaluating the function of macroalgae in biological cycling of carbon (Krause-Jensen & Duarte 2016). The development of methods such as *in situ* experiments allows for better quantification of the function of kelp (Wada et al. 2007, Reed et al. 2015). In the present research, we conducted the study in a semi-*in situ* system using entire kelp individuals and extended the study time through day and night to accurately quantify NPP and DOC production. In the 2 incubations, though the temperature in January was near freezing point, the cultured cold-water kelp species *Saccharina japonica* maintained strong photosynthesis and growth (Zhang et al. 2012) and showed a higher NPP than in April (Fig. 3), when the temperature (Table 1) far exceeded the optimum temperature range of 5–10°C for kelp growth (Zhang 1992). DOC production was 6.2–7.0 mg C (g dry wt)$^{-1}$ d^{-1} (Fig. 4) and was comparable with the release rates of DOC by the uncultured kelp *Macrocystis pyrifera* (about 1.2–4.8 mg C [g dry wt]$^{-1}$ d^{-1}) in Santa Barbara, California, USA in *in situ* incubations (Reed et al. 2015) and with the uncultured *Ecklonia cava* Kjellman, by *in situ* field bag experiments in Oura Bay, Japan (range: 0.12 and 5.8 mg C [g dry wt] d^{-1}) (Wada et al. 2007). NPP values in the present study were higher than those of kelp *Laminaria hyperborea* along the west coast of Norway (Abdullah & Fredriksen 2004), while the fraction of DOC to NPP was comparable (26% along west coast of Norway and 31.4% in the present study). DOC to NPP in our present study also fell within the range of the previous studies for *E. cava* (18–62%, Wada et al. 2007) and 23–62% of the NPP for various macroalgae such as brown, red, and green algae (Khailov & Burlakova 1969, Sieburth 1969, Wyatt et al. 2014). The above compatibility suggests that the release rate of DOC depends on, to some extent, NPP.

There are few studies on the effect of temperature on the release and decay of DOC from macroalgae (Reed et al. 2015, Iñiguez et al. 2016). Existing studies on the phytoplankton DOC response to temperature can provide some comparison. For example, Watanabe (1980) found that DOC to NPP increased when the temperature was too high or too low. Although phytoplankton populations exhibit different temperature response characteristics in different environments or among different phytoplankton species (Watanabe 1980, Verity 1981, Zlotnik & Dubinsky 1989), a common finding of these studies is that DOC to NPP increases only when extreme temperatures inhibit photosynthesis. High temperatures can increase the mobility of cell membrane molecules, which directly leads to an increase in the rate of transmembrane transport of substances (Myklestad & Swift 1998). In our data, DOC to NPP in April was higher than that in January with the insignificant difference due to the variability. A valid explanation would be that the water temperature ranged from 14.7–17.8°C in April far exceeded the optimum temperature range of 5–10°C for kelp growth and photosynthesis (Zhang 1992).The high temperature likely caused the electrolyte permeability of the cytoplasmic membrane to increase and the stability of the membrane to deteriorate;, thus more organic matter synthesized by photosynthesis was released in the form of DOC. Studies also have shown that temperature affects the decomposition rate of BDOC (Middelboe & Lundsgaard 2003, Kirchman et al. 2005, 2009, Lønborg et al. 2009). The lower BDOC decomposition rate in January than in April was due to the lower incubation temperature at which the biological reaction rates were low.

In addition to temperature, light availability (Mague et al. 1980, Verity 1981, Zlotnik & Dubinsky 1989, Mueller et al. 2014) and nutrients (Haas et al. 2010, Barrón et al. 2012) are among the factors that are proposed to alter DOC release rates by primary producers. A similar phenomenon, frequently observed in different studies, is that the absolute amount of DOC increases with increasing light intensity (Zlotnik & Dubinsky 1989). However, when algae deplete the limiting nutrient, cell growth and photosynthetic rates are significantly reduced (Mague et al. 1980, Børsheim et al. 2005), the absolute amount of DOC release decreases, while the DOC to NPP percent increases (Myklestad et al. 1989, Granum et al. 2002). In the April incubation, the higher DOC to NPP may also be related to nutrient depletion (Table 1), where the rate of carbon sequestration exceeds the rate of cellular component synthesis and the excess photosynthetic products actively released as DOC in an overflow mechanism (Konopka & Schnur, 1981, Wood & Van Valen 1990).

Bioavailability is an important factor controlling the dynamics of marine DOC. Previous studies on DOC bioavailability were mostly carried out in relatively short-term cultivation experiments (5–30 d, De

Vittor et al. 2009), and RDOC was not determined (Kirchman et al. 1991, Amon & Benner 1994, Wada et al. 2008). Therefore, k_{DOC} in the former studies cannot be directly compared with our study because RDOC was not included in the degradation model in the former studies (Wada et al. 2008). However, we compared the decomposition proportion at the same time point as in other studies. After 30 d of cultivation, the DOC from kelp was decomposed by about 46.8–51.6%. Our above results are similar to that of Wada et al. (2008), in which 14.3–71.1% was mineralized after 30 d with a mean of 53.7% for the samplings. Compared with the degradation rates of DOC from phytoplankton cultures it appears that DOC from kelp is relatively biorefractory, as the previous results showed that DOC from phytoplankton could be utilized by bacteria within days to weeks (Kirchman et al. 1991, Chen & Wangersky 1996, Hama et al. 2004, Davis & Benner 2007). The difference in the bioavailability may be mainly related to the relatively recalcitrant fucans and humic-like substances from kelp (Wada et al. 2008). After the 150 d decay, 37.3% and 38.2% was left as RDOC in the January and April incubations, respectively. Though limited data was available in quantifying the RDOC from macroalgae, the proportion of RDOC in our study was close to that in a coral reef ecosystem, in which the refractory DOC was 6–37% (average 23%, for 1 yr dark incubation) (Tanaka et al. 2011).

However, it should be pointed out that the conditions in laboratory decomposition experiments are different from those in the field. This is a common limitation of decomposition experiments, because light (Lindell et al. 1995, Moran & Zepp 1997), nutrient supply (Rivkin & Anderson 1997, Kragh & Søndergaard 2009), inoculating (Xiao et al. 2020), dissolved oxygen conditions, and even water extraction during the experiment all potentially affect DOC mineralization and bacterial abundance (Martinez et al. 1996, Arnosti et al. 2005) and may have resulted in a higher DOC refractory fraction in our study. Future studies should focus on how to minimize the limitations of experimental conditions and should include experiments on aspects such as *in situ* decomposition.

Based on the primary production of kelp in the present study and the primary production of phytoplankton in prior research (Table 2), it was calculated that the annual DOC production of kelp and phytoplankton was 470.1 and 41.7 mg C m^{-2} d^{-1}, respectively, on the bay scale. The DOC production from the cultured kelp was up to 11.3 times higher than that of phytoplankton. A similar result was also found in the giant kelp forest at Mohawk Reef, USA, in which DOC production was 500 mg C m^{-2} d^{-1} and was ~2 orders of magnitude greater than the rate of DOC production by phytoplankton (Reed et al. 2015). Higher values of DOC are found in the seaweed-dominated culture area of Sanggou Bay during spring, summer and winter. According to the water residence time, 69.4–91.2% and 34.0–76.1% of kelp DOC production would be exported out of the system in winter and spring, respectively, entering the Yellow Sea. Through osmosis and enzymatic hydrolysis, the DOC from kelp will be converted to bacterial biomass, which can be ingested by microscopic phytoplankton (mainly flagellates and ciliates), and then the energy from kelp production will finally enter the classical food chain via zooplankton such as copepods (Azam et al. 1983). The significance of kelp-derived DOC in coastal waters has been increasingly realized (Newell et al. 1981, Wada et al. 2008, Wada & Hama 2013), and it is suggested that DOC inputs

Table 2. Calculated dissolved organic carbon (DOC) production of phytoplankton and cultured kelp in Sanggou Bay. NPP: net primary production

	Biomass (g DW m^{-2})	NPP (mg C m^{-2} d^{-1})	Proportion of DOC in NPP (%)	Total DOC production (mg C m^{-2} d^{-1})	DOC production for the entire bay (Mg C d^{-1})
Phytoplankton	2.2[a]	180.3[b]	23.1[c]	41.7	6.0
Cultured kelp	65.6[d]	1495.7	31.4	470.1	67.7

[a]Biomass of phytoplankton in terms of chl *a* (Jiang et al. 2017) was converted to dry weight using 50 unit of C = 1 unit of phytoplankton chl *a* (Charpy & Roubaud-Charpy 1990) and a carbon to dry organic matter ratio of 1:2.5 (Parsons et al. 1977)

[b]Primary production taken from Jiang et al. (2017)

[c]Proportion of DOC to NPP as reported by Liu (2012)

[d]Biomass of cultured kelp was calculated by the culture density and individual growth dynamics from Zhang et al. (2012) and the ratio of wet to dry weight from Fang et al. (2020)

from ocean margins to the open ocean interior could be more than an order of magnitude greater than inputs of recently produced organic carbon derived from the surface ocean (Bauer & Druffel 1998).

Kelp farming is rapidly developing in China (China Fishery Statistical Yearbook 2019). Although, in our study, the majority of new DOC from kelp was BDOC and mineralized within months, the remaining RDOC amounted to 37.8%, which may be further transformed by microbes to degraded DOC that is highly resistant to microbial decomposition (Jiao et al. 2010, Lechtenfeld et al. 2015), as was the case of DOC from photosynthetic plankton consumed by heterotrophs and transformed to resistant carbon (del Giorgio & Duarte 2002). Thus DOC from farmed kelp can eventually contribute to carbon sequestration through the microbial carbon pump (MCP) (Jiao et al. 2018), and kelp aquaculture offers a pathway of carbon sequestration and provides a potential method to help fulfill China's mission to reduce greenhouse gas emissions.

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