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Review article

Cultivation of seaweed *Gracilaria* in Chinese coastal waters and its contribution to environmental improvements

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ABSTRACT

Over the past decade, the large-scale cultivation of seaweed *Gracilaria* has expanded rapidly in the Chinese coastal waters. The production of *Gracilaria* increased from 50,536 tons (t, dry weight) in 2003 to 114,722 t in 2010. The production of the seaweed ranks third only to kelps *Saccharina* (formerly referred to as *Laminaria*) and *Undaria* in China. Nan'ao located in Shantou City, Guangdong Province has been successfully developed as one of the major cultivation bases of *Gracilaria lemaneiformis* at an industrial scale in South China since 2000, and the farmed area increased by 11,538-fold from 0.13 ha in 2000 to 1500 ha in 2011. From lab-scale study to field industrial practice, it has been documented that *Gracilaria* cultivation is beneficial in environmental improvements such as mitigating eutrophication, controlling harmful algal blooms, maintaining healthy mariculture systems, and sequestrating CO_2. *Gracilaria* may significantly remediate contaminants in mariculture ecosystems and improve the water environment, and its cultivation provides a new approach to coastal environmental improvement in China and the world.

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1. Introduction

Approximately 1000 seaweed species globally distributed, from cold, temperate to tropical zones, are economically valuable [1]. Those seaweeds play very important roles in sustaining the biodiversity and ecological functions in marine ecosystems [2]. More than 100 species of *Gracilaria* have been described in the world, and they grow mostly in temperate, subtropical and tropical zones [3,4]. Historically, seaweeds are harvested from nature. However, seaweed cultivation has significantly grown rapidly since the early 20th century due to the continuously rising demand for food and industry. Several species of algae have been cultivated for many years, especially *Pyropia* (formerly referred to as *Porphyra*), *Saccharina* (formerly referred to as *Laminaria*), and *Nostoc* for food, *Gloipeltis* for colloidal substances and *Gracilaria* for feedstuffs and agar materials [5].

Cultivation of seaweed is one type of aquaculture. Now, aquaculture is growing fastest in the food production sector, and its average annual growth rate reached 8.3% between 1970 and 2009, compared to that of 4.9% for poultry, 2.9% for pig, and 1.8% for sheep and goats [6]. China has had the highest mariculture production in the world for over 20 years, and has remained one of the most important contributors to the world aquaculture production. For example, its mariculture production in 2010 reached 14.82 million t and accounted for 44.2% of the world's total production [7].

The rapid development of mariculture has resulted in an increasing release of nitrogen (N) and phosphorus (P) into the mariculture and its surrounding ecosystems. For example, Troell et al. [8] found that more than half of nutrients originated from marine fish culture systems, with the contribution of P, carbon (C) and N approximating 85%, 80–88% and 52–95%, respectively. Excess feed and fecal wastes of cultivated animals settle to the bottom through the water column, and then are incorporated into sediments, where the remineralization of particulate organic matter may cause an increase in dissolved inorganic nutrient concentrations. Increased discharge of organic pollutants from aquaculture farms may lead to various adverse effects to local environments, such as eutrophication, anoxia, loss of biodiversity, and coastal-water pollution [8,9].

Mixing cultivation, which incorporates seaweeds into animal mariculture systems, has long proven to be the most promising approach for mitigating the pollution of the surrounding environment by aquaculture operations. Accordingly, seaweed cultivation has been carried out for decades and has grown rapidly in China and other countries [8, 10–12]. The seaweeds cultivated at an industrial scale include many species, such as *Saccharina*, *Pyropia*, *Undaria*, and *Gracilaria* species in China.

This paper reviews the history and presents the status of *Gracilaria* cultivation, its potential environmental importance as eco-materials, and its role in maintaining healthy mariculture ecosystems in the Chinese coastal waters.

2. Species diversity of the genus *Gracilaria* and its distribution in China

There are more than 30 species in the genus *Gracilaria* in China [1, 13]. They distribute in the coastal waters from Liaoning in the north to Hainan in the south of China (Table 1). Species diversity of *Gracilaria* is higher in the south than in the north, and almost 50% of *Gracilaria* species are found in Guangdong and Hainan Provinces in the southern China. In the genus *Gracilaria*, the most economically important species is *Gracilaria lemaneiformis* based on the recent 10-year documentation, which contributes the most to the production of *Gracilaria* in China.

3. Mariculture development of seaweed *Gracilaria* and economical animals

3.1. Gracilaria cultivation

The artificial cultivation of *Gracilaria* began in the 1950s in China, but then the production was low. For example, the production of *Gracilaria tenuistipitata* and other *Gracilaria* species was about 500 t (fresh weight) per year in the late 1950s. By the end of the 1980s, the area for *Gracilaria* cultivation in South China reached 2000 ha, with an annual yield of 3000 t (dry weight) [1].

The cultivation history of *Gracilaria* in China may be divided into 2 stages. From the 1950s to 2000, the main cultivation species was *G. tenuistipitata*. This seaweed was cultivated mostly in ponds in small scales (just several ha), and its total production was low and not even recorded in the Chinese Statistical Yearbook of Fisheries. Starting from 2000 to 2002, the cultivation of *G. lemaneiformis* was experimentally carried out in Nan'ao, Guangdong Province. The biomass of this seaweed increased by 282-fold (from 15 g m^{-1} to 4230 g m^{-1}) over a 155-day period, showing a much faster growth rate than *G. tenuistipitata*. Thus *G. lemaneiformis* was experimentally proven to be a good candidate for industry-scale cultivation in China. From 2003 to 2012, the cultivation

Table 1
The distribution of *Gracilaria* species among the Chinese coasts [1,11,13].

Species	Distribution
G. lemaneiformis Bory	Shandong, Liaoning, Guangdong, Fujian
G. gigas Harvey	Guangdong, Fujian
G. tenuistipitata Zhang et Xia	Guangdong
G. tenuistipitata Var. *liui* Zhang et Xia	Guangdong, Guangxi, Hainan, Fujian, Zhejiang
G. asiatica Zhang et Xia	Chinese coast
G. asiatica Var. Zhang et Xia	Fujian, Guangdong
G. chouae Zhang et Xia	Fujian, Zhejiang
G. chorda Holmes	Hainan
G. salicornia (Ag.) Dawson	Guangdong, Hainan, Taiwan
G. articulata Chang et Xia	Hainan
G. arcuata Zanardini	Hainan
G. blodgettii Harvey	Fujian, Taiwan, Guangdong, Guangxi, Hainan
G. changii (Xia et Abbott) Abbott Zhang et Xia	Guangdong, Guangxi
G. bangmeiana Zhang et Abbott	Hainan
G. bailinae Zhang et Xia	Guangdong, Hainan
G. megaspora (Dawson) Papenfuss	Fujian
G. spinulosa (Kam) Chang et Xia	Hainan, Taiwan
G. textorii (Suring) De Toni	Liaoning, Shandong
G. eucheumoides Harvey	Taiwan, Hainan
G. rubra Chang et Xia	Hainan
G. hainanensis Chang et Xia	Hainan
G. firma Chang et Xia	Guangdong, Guangxi
G. filiformis Harvey Baily	Hainan, Taiwan
G. cuneifolia Lee et Kurogi	Hainan
G. edulis (Gmelin) Silva	–
G. fanii Xia et Pan	Guangdong
G. glomerata Zhang et Xia	Hainan
G. longirostris Zhang et Wang	Guangdong
G. yinggehaiensis Zhang et Xia	Hainan
G. yamamotoi Zhang et Xia	Hainan
G. punctata (Okamura) Yamada	Taiwan
G. mixta Abbott, Zhang et Xia	Guangdong

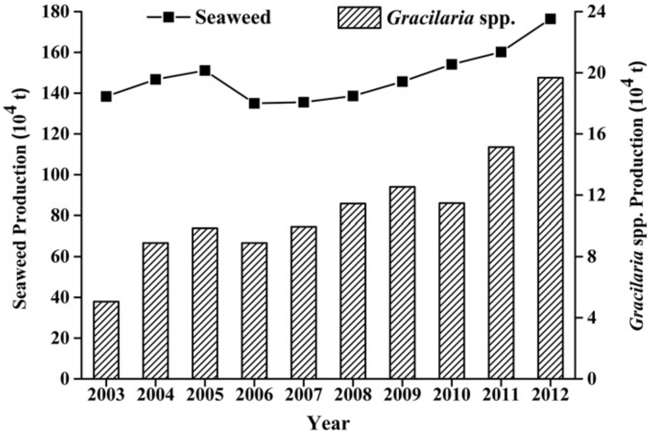

Fig. 1. The development of seaweed and *Gracilaria* cultivation in China during 2003–2012. Data from the State Oceanic Administration, China [14] and China Fishery Statistical Yearbook [15].

of *G. lemaneiformis* at industrial scales expanded rapidly in Guangdong, Fujian, Shandong and other Chinese coastal waters. Its production increased from 50,536 t in 2003 to 196,778 t (dw) in 2012 (Fig. 1), and since then, this seaweed species has become the largest contributor to *Gracilaria* production [11,12].

Nan'ao County is an island located in the east of Guangdong province with about 5000 out of its 70,000 population now engaged in the *Gracilaria* cultivation industry. Nan'ao is a good example of the recently rapid development of *Gracilaria* cultivation. Its cultivation area increased from 0.13 ha in 2000 to 1500 ha in 2011 (Fig. 2), and the annual yield increased from 4 t to 60,000 t (wet weight).

Among the genus *Gracilaria*, the most commonly cultivated species is *G. lemaneiformis* due to its fast growth and high yield. In most cultivation waters, its daily specific growth rate is over 10% (Table 2). The two most popular methods for *Gracilaria* cultivation in China are pond-scattering and floating raft cultures (Table 3). Pond-scattering is more suitable for species from which sporelings are easy to obtain, with *G. tenuistipitata* as a good example. The floating raft method for *G. lemaneiformis* is adapted from *Saccharina* farming and has been used in most Chinese coastal areas since 2000 [11,12,16].

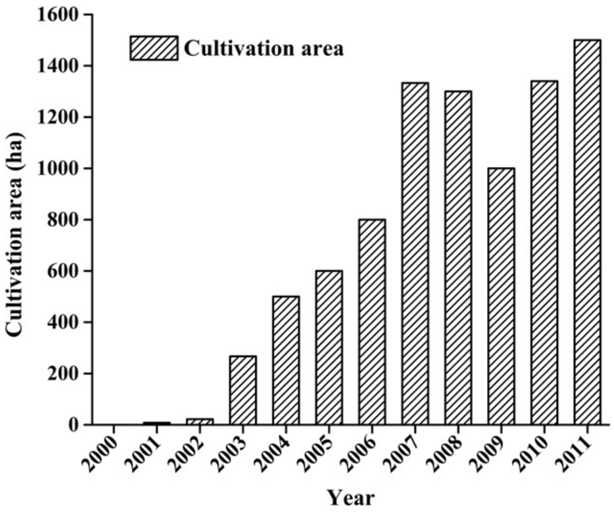

Fig. 2. The development of *Gracilaria* cultivation in Nan'ao, Guangdong Province, China during 2000–2011.

Table 2
The different specific growth rates (SGRs) of *G. lemaneiformis* in Chinese coastal waters.

Site	Growth period	SGR (%/day)	References
Net cages in Nan'ao	Nov 17–Dec 20, 2001	11.71	[12]
Jiaozhou Bay	Oct 2–30, 2001	13.90	[12]
Jiaozhou Bay	Jun 13–Jul 12, 2004	11.30	[16]

3.2. Mariculture of economically important animals

Large-scale mariculture of economically important animals in China began in early 1980s. Mariculture systems are usually developed in shallow coastal waters. The cultured animals are mostly fish, shellfish, shrimps and crabs, generally farmed in cages or on rafts. Of the total mariculture production during 1999–2001, the cultivated animals accounted for 88.7%, while that of algae was only 11.3% [20].

According to the data from China Ocean Yearbook and the China Fishery Statistical Yearbook, mariculture production increased year by year from 1954 to 2010 in China (Fig. 3), and the annual production was only 153,700 t in 1954. Since 1980 increased mariculture activities have emerged to meet the demand for seafood and industrial use, and the annual yield soared to 801,700 t in 1981, 3,333,100 t in 1991, and 14,823,008 t in 2010. The annual yield in 2010 was 91.4 times of that in 1954, and 17.5 times of that in 1981.

From 1967 to 1980, kelps made up more than half of the total mariculture production, and the production of *Laminaria japonica* (now renamed as *Saccharina japonica*) ranked first in 1980, reaching 252,907 t (dry wet). Later, the proportion of kelps decreased gradually with the increased production of molluscs, shrimps and finfish. During 1999–2001, almost 90% of the mariculture production was from economically important animals, such as shellfish and finfish [20]. Consequently, the production of cultivated animals led well ahead of algal cultivation, resulting in unbalanced mariculture ecosystems in China. The rapid development of aquaculture as well as the associated changes in major species cultivated has led to increasing concerns about the impacts of mariculture on the coastal environment. The increase in nutrients released from excessive fish feed and cultured animal wastes has been well documented as the most important cause of eutrophication. It has also been suggested that the resulting increase in nutrient inputs may lead to an elevated frequency and extensiveness of harmful algal bloom (HAB) due to high stocking densities of animals, such as fish and shellfish [9,19,22,23].

The incorporation of seaweed into animal mariculture systems has proven to be the most promising approach for mitigating eutrophication of the surrounding environment polluted by aquaculture [8,10,23]. During the growth period, *G. lemaneiformis* and other seaweeds were very effective in mitigating eutrophication and inhibiting the growth of some microalgae [11,12,24]. Therefore, the cultivation operation of *Gracilaria* is very beneficial for the improvement of economy and environment. Meanwhile, the seaweed can be used as seafood, feed for abalone, and/or agar materials after it is harvested. This is why the cultivation of *G. lemaneiformis* at industrial scales has been encouraged by the local government, and consequently expanded rapidly in China.

Table 3
Main species of *Gracilaria* cultivated in Chinese coastal waters.

Species	Cultivation mode	Site	References
G. gigas	Raft culture	Fujian	[17]
G. tenuistipitata var. *liui*	Pond-scattering culture	Guangxi	[18]
G. lemaneiformis	Raft culture	Fujian, Guangdong, Shandong	[11,12]
G. verrucosa	Raft culture	Zhejiang	[19]

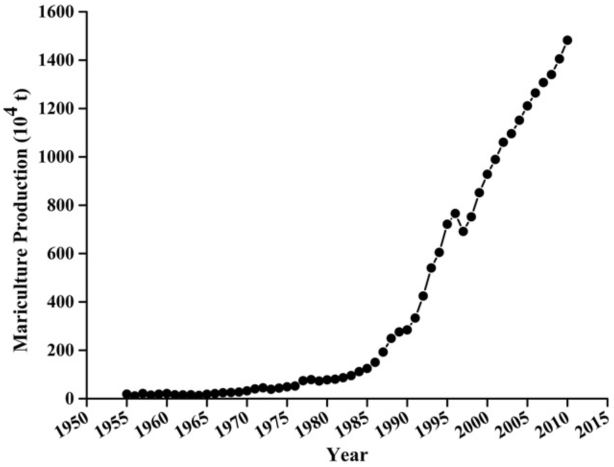

Fig. 3. Temporal variation in mariculture production since 1954 in Chinese coastal waters. Data from China Ocean Yearbook [21] and China Fishery Statistical Yearbook [15].

4. Main environmental factors influencing *Gracilaria* cultivation

Several key environmental factors have been identified to affect *Gracilaria* cultivation, including light, temperature, salinity, nutrients, cultivation depth, water movement, and herbivorous fish and epiphytes.

4.1. Light

Light is one of the most important environmental factors influencing seaweed growth. *Gracilaria* generally requires a high light intensity for normal growth, and the optimal illumination intensity for *G. lemaneiformis* is 40–60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ [25,26]. However, when seaweed is farmed in the sea, either hung horizontally at various depths in most cases or sometimes vertically in the water column, they are subjected to a large fluctuation of irradiance availability due to the water depths, daytime and self-shading. Some seaweed species seem to be able to acclimate their photosynthetic characteristics to conditions above or below the optimal irradiance ranges. They adapt to such environmental fluctuations with a higher, genetically fixed potential for photosynthetic acclimation, enabling them to turn their photosynthetic characteristics in concert with the changes of light levels in their natural habitat. For example, *Mazzaella laminarioides* employed almost exclusively a physiological acclimation of the photosynthetic apparatus, while *Gracilaria chilensis* lacked any sign of acclimation of the main photosynthetic parameters, and *Sarcothalia crispata* relied on both physiological adjustment of the photosynthetic apparatus and morphological acclimation [27]. Xu and Gao [28] studied the response of *G. lemaneiformis* to reduced solar radiation at increased depths. They found that this seaweed increased cellular contents of the photosynthetic pigments (e.g., *Chl a*, phycoerythrin), and decreased the content of ultra-violet absorbing compounds (UVACs) to acclimate the low solar radiation. This strategy can enable the alga to capture more light for photosynthesis and to reduce the metabolic cost of the production of the secondary products, UVACs. However, it appeared that a general pattern for photosynthetic acclimation in seaweeds to different light levels was not evident.

4.2. Temperature

Temperature has an important influence on the seasonal and geographic distribution, and the growth rate of *Gracilaria*. Most species grow well at 20 °C or above, but some have an upper limit beyond which production may be reduced or even cease. Production may also be severely limited by low temperatures [29]. Under the conditions of nutrient-enriched seawater cultivation, the daily SGR of *G. coronopifolia* was positively correlated with temperature ranging from 15 to 35 °C, reaching a maximum production rate at 30 °C [30]. The favorable temperature for *G. lemaneiformis* growth ranged from 12 to 23 °C. When the water temperature is lower than 10 °C, the average SGR of *Gracilaria* species becomes negative; when water temperature is over 26 °C, the seaweed dies. So the growth period of *G. lemaneiformis* is about six months, generally from November to April in Nan'ao, Shantou. Water temperature controls the growth of this seaweed, thus it is one of the most important limiting factors. In contrast to *G. lemaneiformis*, the subtropical species *G. tenuistipitata* var. *liui* grows fastest at 20–30 °C in natural seawater ponds, but its growth rate decreases at temperatures below 15 °C or over 32 °C [18]. In addition, temperature may also influence several physiological processes in algae, such as diffusive rates and carrier-mediated nutrient uptake. For example, the NO_3^- uptake rate of *G. tikvahiae* was found to increase with increasing temperatures [31].

4.3. Salinity

Salinity is a particularly important factor influencing the growth of *G. tenuistipitata* var. *liui*. This species grows well in estuaries or ponds where salinity is low and N content is high [1]. In a field survey in Zhuhai City, China, we found that *G. tenuistipitata* var. *liui* was able to survive at a salinity of 5 PSU. *G. lemaneiformis* is able to grow across the salinity range of 15-35 PSU in south Chinese coastal waters (unpublished data).

4.4. Nutrients

Nutrient availability has an important influence on the growth of *Gracilaria*. Nutrient concentrations in Chinese coastal waters tend to be higher in the south than in the north, because there are more rivers in the south bringing N and P rich terrestrial runoff to the sea [1]. It has been shown that the growth rate of *G. tenuistipitata* var. *liui* was the highest when concentrations of total inorganic N reached 4 μmol/L [18]. Among nutrients, ammonia plays a very important role in controlling the growth of *Gracilaria*. For example, a previous study demonstrated that biomass production in *G. parvispora* was positively correlated with ammonia concentrations within the range of 0.2–4.0 μM, but exhibited insignificant correlations with any other water quality factors, such as NO_3^- or PO_4^{3-} concentrations [32]. Another study also concluded that the seaweed growth accelerated when the N/P concentrations increased from 50/3.13 μM to 400/25 μM, but decreased significantly when the N/P concentrations exceeded 400/25 μM [33].

4.5. Cultivation depth

Cultivation depth is an important, complex factor that determines the productivity of seaweeds due to its negative correlation with light intensity. *Gracilaria* productivity varies with cultivation depth, increasing from 84 t ha^{-1} $year^{-1}$ at 0.75 m to 132 t ha^{-1} $year^{-1}$ at 1.5 m but decreasing to 128 t ha^{-1} $year^{-1}$ at 2.5 m [34]. Wu et al. [18] found that 30 cm was the optimum cultivation depth for *G. tenuistipitata* var. *liui* in pond cultivation. The cultivation experiment of *G. lemaneiformis* in the Jiaozhou Bay, China showed that the greatest rates of increase in *Gracilaria* biomass were observed under horizontal cultivation (i.e. at the seawater surface), followed by a vertical cultivation at water depths of 0.5–1.5 m, 0–1.0 m, and 1.0–2.0 m, respectively, while the lowest biomass was found at 1.5–2.5 m below the surface [12]. Based on previous data, the optimum depth for *Gracilaria* thallus to achieve the maximum biomass was 0–1.0 m, where the maximum growth rate was over 11% per day [12].

4.6. Water movement

Water movement accelerates the diffusion rates of gases and nutrients in and out of the seaweed thalli, creating favorable environmental conditions for the rapid growth of *Gracilaria*. Water movement is generally three to four times lower in cultivation tanks as compared to natural lagoons, but the water–air exchange remains almost at the same rate [35]. Insufficient light and water motion have been found to limit the growth of seaweeds. For example, *G. parvispora* grew at much lower rates in tanks (2.6% day^{-1}) than in a lagoon (8–10% day^{-1}) [35]; when nutrients were sufficient, water flow became an important limiting factor controlling the growth of *G. parvispora* thalli [36]. In general, water motion exerts significant effects on the growth of *Gracilaria*.

4.7. Herbivorous fish and epiphytes

Seaweed abundance and biodiversity are influenced by herbivores and other organisms. Primary consumption by herbivores can reduce the thallus mass of seaweeds, and thus strongly influence the growth and reproduction of seaweeds [37,38]. One of the greatest challenges in *Gracilaria* cultivation is the grazing by herbivorous fish and epiphytes. The impact of grazers may fluctuate and even cause a complete loss of seaweed production. As observed in the Jiaozhou Bay, Shandong Province, production loss from epiphytic growth on *Gracilaria* was negligible (<3% total biomass) throughout the cultivation period [12]. In contrast, the fish *Siganus canaliculatus* immigrates to the cultivation area of *Gracilaria* in the Nan'ao Island, Guangdong from May to October each year when the water temperature exceeds 20 °C, and feeds devastatingly on *Gracilaria*. Thus, the favorable season for *Gracilaria* cultivation in Nan'ao is from January to April, when the water temperature falls between 15 and 20 °C. In some sea areas of South China, it is very difficult to cultivate *Gracilaria* because there are too many *S. canaliculatus* living in the coastal waters throughout the year. The herbivorous fish is the most important factor affecting *Gracilaria* cultivation industry in the South Chinese sea areas such as Zhuhai and Yangjiang, Guangdong Province.

5. Bioremediation potential of *Gracilaria* for environmental improvement

As an efficient nutrient pumper, *Gracilaria* may be used in integrated aquaculture systems to reduce eutrophication, control red tides, remediate contaminants and sequestrate CO_2 [11,12,23,39,40]. All those will contribute to the improvement of coastal water environments. Seaweeds also create habitats, providing shelters and serving as feeding/nursery grounds for many organisms, which helps protect the diversity of marine organisms [41,42]. Furthermore, seaweed aquaculture beds can play important roles in dampening waves [43], absorbing excess nutrients [11], and buffering ocean acidification [44], and potentially serving as a sink for anthropogenic CO_2 [45–47]. *Gracilaria* cultivation improves environmental quality in many aspects, and below we mainly focus on its contribution to maintaining healthy mariculture systems, controlling harmful algal blooms, and potentially mitigating global warming.

5.1. Maintaining healthy mariculture systems

A large-scale cultivation of *Gracilaria* provides many benefits for the maintenance of healthy mariculture ecosystems, including nutrient removal, inhibition the growth of phytoplankton and harmful algae, and increase in dissolved oxygen (DO) of the water.

5.1.1. Nutrient removal

In most aquaculture systems in China, economically important animals, such as fish and shrimps are usually cultivated in coastal enclosures or land-based tanks. The “fed” animals are enclosed, so their wastes release abundant nutrients during decomposition and thus pollute the cultivation and surrounding waters. By contrast, seaweeds can make biomass out of nutrient-rich effluents and when harvested, they may become aquaculture feed, seafoods, or materials for the pharmaceutical industry. Thus, the integration of seaweeds into animal mariculture systems not only contributes significant extra revenues to the aquaculture industry, but also addresses environmental concerns [10,23,48,49].

Cultivated seaweeds grow very fast under higher N concentrations than any other nutrients [11,50]. The use of seaweeds to treat mariculture effluents was first developed in the mid-1970s, and recently has been increasingly adopted in intensive and semi-intensive mariculture systems. It has been shown that integrating animal mariculture systems with seaweed production significantly reduces the total discharge of dissolved nutrients to the environment [40,51,52]. Field experiments also demonstrated that 1 ha cultivation of *G. chilensis* removed more than 5% of the dissolved inorganic N, and 27% of the dissolved P released from the nearby salmon cages [52,53].

An aquarium experiment integrating fish with seaweeds further demonstrated that *G. lemaneiformis* could effectively remove nutrients from the integration system. In the aquaria with *G. lemaneiformis*, NH_4-N and PO_4-P concentrations decreased by 85.5% and 66.0% (after 23 days), and by 69.5% and 26.7% (after 40 days), respectively. In enclosed experiments, *G. lemaneiformis* could remove NH_4-N, NO_3-N and NO_2-N by 68.44%, 23.03% and 13.04%, respectively during a 24-h period [12]. Similar experiments with *G. verrucosa* grown within *Lateolabrax japonicus* fish cages were conducted at the Xiangshan Harbor; after 45 days, the average concentrations of PO_4-P, NO_2-N, NO_3-N and NH_4-N in the fish cages were reduced by 22–58%, 24–48%, 22–61% and 24–71%, respectively [23]. It is now well established that the maximum uptake rate by *G. lichenoides* was 55.88 $\mu\text{mol g}^{-1}\text{ h}^{-1}$ for NO_3-N, 35.17 $\mu\text{mol g}^{-1}\text{ h}^{-1}$ for NH_4-N, and 3.106 $\mu\text{mol g}^{-1}\text{ h}^{-1}$ for PO_4-P; and the corresponding maximum uptake rates by *G. lemaneiformis* were 53.17, 32.24 and 3.064 $\mu\text{mol g}^{-1}\text{ h}^{-1}$, respectively [54]. These findings indicate that *Gracilaria* is a good biofilter for removing nutrients. Therefore, integrating seaweed cultivation with fish mariculture systems has promising economic and environmental advantages. Seaweeds may be used as a biofilter in eutrophic sea waters.

Integrated multi-trophic aquaculture (IMTA) strategies have been considered as a key development for aquaculture sustainability and bioremediation potential. Seaweeds strip N and P released from fish wastes to the water column, gaining nutrients for their growth and meanwhile removing organic pollutants from aquaculture [55]. Practice has proven that *Gracilaria* species are very valuable for enhancing aquaculture waste treatments and for in situ bioremediation of contaminated water environments in China [12,23] and other countries [56,57].

Using seaweeds to clean nutrient-rich effluents from monocultures of marine animals is considered as an effective and environmentally friendly method for waste management. A 1-ha co-cultivation of *G. lemaneiformis* and fish in Northern China yielded more than 70 t of fresh seaweed annually, equivalently sequestrating 2.5 t C and removing 0.22 t N and 0.03 t P from the seawater [16]. To balance the side effects and eventually eliminate the eutrophication by scallop cultivation, an industrial scale cultivation of seaweeds has been encouraged in Northern China [11].

5.1.2. Increased dissolved oxygen levels

The oxygen produced by *Gracilaria* through photosynthesis can be used to improve the respiration of cultivated animals, such as fish and prawns, and to oxidize H_2S. Compared to marine fish cages without seaweeds, the concentration of DO within an integrated system (*Gracilaria* + fish) increased by 28%, and the transparency of the seawater increased by 30% while chlorophyll *a* decreased by 49% [19].

Seventeen surveys were carried out in the sea water cages (3 m × 3 m) and the surrounding waters of Nan'ao from November 17 to December 13, 2002. The results revealed that the highest DO values were observed within the cages with *Gracilaria* ($6.60 \pm 0.62\ \text{mg L}^{-1}$), the second highest values in the surrounding seawaters outside the cages ($6.36 \pm 0.68\ \text{mg L}^{-1}$), and the lowest values in the fish cages without this seaweed ($6.28 \pm 0.72\ \text{mg L}^{-1}$) ($p > 0.05$, unpublished data From Yang Y F Research Group). Although the difference is not significant, possible resulting from the close distance between sampling sites (3 m) and the high water exchange rate through the fish cage holes. In a 9-day mesocosm ($1.0\ m^3$) experiment carried out at Nan'ao Experimental Station, Shantou University in December 2005, it was found that the DO concentrations (monitored by YSI-556, USA) in the mesocosms with *Gracilaria* ($13.13 \pm 4.08\ mg\ L^{-1}$) were higher than those without seaweeds ($10.51 \pm 2.6\ mg\ L^{-1}$) ($p > 0.05$, unpublished dada from Yang Y F Research Group). Tang et al. [58] demonstrated that DO concentrations in the sea area with *Gracilaria* were higher than those without seaweed. These results suggest that the cultivation of *Gracilaria* is an effective way for improving DO levels in seawaters.

Among seaweeds, *G. lemaneiformis* is a high-yield seaweed that can be refined for commercially valuable products, and thus it is a very effective eco-material for increasing DO and nutrient removal in the mariculture areas. Seaweed filtration can potentially improve the efficiency and productivity of recirculating aquaculture systems, help keep the water clean in the IMTA systems, and maintain the health of mariculture systems [12,23,48].

5.2. Inhibitory effects of Gracilaria on phytoplankton and harmful algal bloom species

Diverse harmful algal bloom (HAB) species increasingly threaten fisheries and aquaculture, as well as the health and diversity of coastal ecosystems. Increased frequency of HAB occurrence has become a serious environmental problem in Chinese coastal waters, particularly in some mariculture areas. Biological strategies have been suggested for the potential mitigation of HABs with few side effects. The collective research has demonstrated that *Gracilaria* is able to inhibit the growth of phytoplankton including HAB-causing species.

5.2.1. Phytoplankton community structure

To test the inhibitory effects of cultivated *G. lemaneiformis* on phytoplankton community structure, a 12-day mesocosm experiment ($1.0\ m^3$) was carried out in the Nan'ao Experimental Station of Shantou University in 2006, and revealed that *G. lemaneiformis* adversely affected the growth of microalgae. The phytoplankton showed a ~35-fold increase in cell density (from 3.017×10^4 to 105.5×10^4 cells L^{-1}) in the mesocosms without *Gracilaria*, in contrast to the only 4-fold increase (from 2.387×10^4 to 26.5×10^4 cells L^{-1}) in the mesocosms with *Gracilaria* during the experimental period (unpublished data).

A field survey in the Nan'ao mariculture area was conducted from April 21 to May 6, 2012. During the survey, 5 visits at 2–3 day intervals were made at six sampling sites (three sites with *Gracilaria*, and three control sites without *Gracilaria*). The results showed that the mean density of phytoplankton was significantly lower in the *Gracilaria* cultivation areas (4.7×10^5 cells L^{-1}) than in the areas without seaweed (8.3×10^5 cells L^{-1}) ($P < 0.05$). Another study carried out in the mariculture area demonstrated that *G. tenuistipitata* was able to depress the development of red-tide microalgae [58]. Therefore, these studies indicate that *Gracilaria* could potentially control phytoplankton growth on a sea-based scale.

5.2.2. Harmful algal bloom species

Food chain transmission results in toxin accumulation in shellfish and fish, consequently increasing the risk of human poisoning, which causes major economic losses and irreversible damages to aquaculture ecosystems [59]. Accordingly, it is very important to decrease microalgal densities and control HAB species in mariculture ecosystems. Biological strategies (e.g., seaweed integration) have been suggested as a potential instrument to prevent, control, and mitigate HABs with few side effects [60–62]. Some seaweed-based integrated mariculture systems have been advocated as an option for sustaining coastal aquaculture systems [10,23].

A study of nutrient competition between two co-existing species, the seaweed *G. lemaneiformis* and the microalga *Prorocentrum donghaiense* showed that the former had obvious algicidal effects on the latter, leading to the complete eradication of *P. donghaiense* algal cells by the end of the experiments [63]. In another experiment carried out in Qingdao, China found that the growth of four selected microalgal species (*P. donghaiense*, *Alexandrium tamarense*, *Amphidinium carterae*, and *Scrippsiella trochoidea*) was inhibited significantly when they were grown with the fresh thalli of *G. lemaneiformis* [39].

The effect of *G. lemaneiformis* on two red tide forming microalgae, *Chaetoceros curvisetus* and *S. trochoidea* was studied by culturing them together in a series of indoor experiments, and the results showed that *Gracilaria* altered the morphology of the red tide forming phytoplankton cells, which became shrunken and suppressed [64]. The higher the initial biomass of *G. lemaneiformis*, the lower was the achieved maximum cell density of *C. curvisetus* and *S. trochoidea*. Consequently, Liu et al. [64] concluded that *G. lemaneiformis* inhibited the growth of these HAB-forming microalgae. This inhibition reportedly involves two aspects. The first is that these macroalgae have high uptake rates of inorganic nutrients, and their strong competition for nutrients and other resources decreases N availability for phytoplankton, and the second is that macroalgae inhibit the growth of phytoplankton by excreting allelopathic substances. Through these mechanisms, *Gracilaria* species play an important role in controlling phytoplankton, especially HAB-forming microalgae [39,65,66].

Many other experiments also have demonstrated that *Gracilaria* species are inhibitory to the growth of red tide microalgae (Table 4). These findings indicate that the cultivation of *Gracilaria* is one of the most effective biological strategies for mitigating HABs.

5.3. Potential as a CO_2 sink

Anthropogenic consumption of fossil fuels and deforestation has raised the atmospheric CO_2 concentration by some 25% since the Industrial Revolution. The atmospheric CO_2 level is predicted to reach 1000 ppm by 2100 [68]. The combustion of coal, petroleum and natural gas by mankind on a large scale releases annually 6000 million t of C into the atmosphere and has now become the main source of gas-inducing greenhouse effect. How to reduce the atmospheric CO_2 level is now a major concern in the scientific community as well as in the international society. It is commonly believed that terrestrial plants are a good CO_2 sink by converting gaseous CO_2 to organic carbohydrates through photosynthesis, thus decelerating global warming. People usually rely on land plants, but not aquatic plants, to sequester CO_2. So far little attention has been paid to the C sequestering effects of seaweeds, although these are globally distributed with a great abundance both naturally and in large-scale cultivation, and, as land plants, have the ability to fix CO_2 efficiently in coastal waters.

Table 4
List of red tide microalgal species inhibited by *Gracilaria*.

Inhibited red tide species	Inhibitory effects	References
Prorocentrum donghaiense	Final cell numbers reduced 100% compare to initial	[39]
	Entirely extinguished	[63]
Heterosigma akashiwo	Completely killed at 120 h	[65]
Scrippsiella trochoidea	Inhibitory rate was 87.5%	[64]
	Final cell numbers reduced 79% compare to initial	[39]
Alexandrium tamarense	Inhibitory rate reached up to 93.1%	[66]
	Final cell numbers reduced 24% compare to initial	[39]
Dunaliella salina	Inhibitory rate reached up to 99.8%	[66]
Skeletonema costatum	Inhibitory rate reached up to 99.1%	[66]
	Cell membrane, chloroplast, mitochondria and nucleolus were damaged	[67]
Prorocentrum micans	Inhibitory rate was 76.7%	[66]

Table 5
Estimated annual carbon absorption and potential CO_2 sequestration by the major seaweed aquaculture species in China in 2012.

Species	Algae harvested (t dw year^{-1})	Percentage of C content (%)	C absorption (t dw year^{-1})	CO_2 sequestration (t dw year^{-1})
Saccharina	979,006	25–31	274,121	1,006,027
Undaria	175,121	31	54,287	199,235
Gracilaria	196,778	31.3	61,592	226,041
Pyropia	112,329	27.3	30,666	112,543
Sargassum	11,226	33–37	3929	14,420
Gelidium	412	36–40	157	574
Total	1,474,872	–	424,752	1,558,840

C absorption by the amount of CO_2 measured in 1 g of dry plant material is 3.67 [76,77]. Data for algae harvested are derived from China Fishery Statistical Yearbook [15]. The C contents in seaweed are from Widowati et al. [73], Muraoka [74], and McVey et al. [75].

Seaweeds are widely distributed in shallow seawaters, either on rocks below the sea surface or in the intertidal zone around continents or islands. Their abundance depends on temperature, light, nutrient condition and water movement. When conditions are suitable, seaweeds can accumulate a large amount of biomass within some area. Biomasses as high as 30–120 t/ha have been recorded in brown and red seaweeds [11,69].

CO_2 diffuses in the seawater at 1/10,000 of the rates in the air [70]. Because injection, aeration, and accelerated water flow increase the availability of CO_2 in aquatic ecosystems, these methods have been adopted to improve yields in many intensive seaweed cultivation systems. An early study showed that the average growth rate of *G. chilensis* thalli increased by over 14% per day when aerated to 1250 ppm CO_2, while the control thalli aerated with natural air alone exhibited an increase of growth rate by only about 9% per day [71]. Another study used flue gases discharged from a power plant (containing 12–15% CO_2) to cultivate *G. cornea*. During the 13-month-long period, this seaweed showed growth rates comparable to those cultivated with commercial CO_2 (weekly biomass increments of 94.1% vs. 91.3%), suggesting that cultivation of *Gracilaria* with power-plant effluents may be a new environmentally friendly way of sequestrating CO_2, and at the meanwhile the seaweed biomass can be converted into biofuels [72].

Annual carbon emission into the atmosphere has increased by 6000 million t in recent years. The current annual worldwide production of seaweeds through cultivation amounts to 6–10 million t of wet biomass, which equates to 0.24–0.4 million t of C. To balance 20–60 million t of C that is equivalent to 0.33–1% of the annual increase of CO_2 added to atmosphere, 670–2000 million t of fresh seaweed biomass need to be cultivated, which is 33–200 times greater than the present cultivation scale. The carbon contents in harvested seaweed dry weight vary among species. For example in *Kappaphycus*, the range of C content was from 20.73 to 43.10% [73]. The C content was 25–31% in *Saccharina*, 32–34% in *Ecklonia*, 33–37% in *Sargassum*, 36–40% in *Gelidium* [74], and 27.3% in *Pyropia* [75]. The algal harvests, annual C absorption and potential CO_2 sequestration by the major seaweed aquaculture species in China in 2012 were shown in Table 5. It can be seen that the large-scale seaweed cultivation may contribute somewhat to sequestration of CO_2 and thereby mitigation of CO_2-induced global warming.

The percentage of C content in harvested *Gracilaria* dry weight (dw) is 31.3% [11]. The sequestered amount of CO_2 was calculated by multiplying 'C absorption' by the amount of CO_2 measured in 1 g of dry plant material which is 3.67 [76,77]. In China in 2012, the production of *Gracilaria* was 196,778 t (China Fishery Statistical Yearbook 2013), potentially sequestrating 226,041 t of CO_2. Therefore, *Gracilaria* cultivation can be regarded as an alternative C sink industry for its high C content, which is quantifiable and controllable during the cultivation process [78].

6. Final considerations and conclusions

Mariculture has undergone a rapid development in China during the last three decades. The annual production reached 14, 823,008 t in 2010, making China the largest mariculture producer in the world. As the production increases, the nutrient concentrations of mariculture waters in China have been continuously rising for several decades [20]. Because *Gracilaria* species are environmentally friendly and economically important, the cultivation of these seaweeds at an industrial scale has been encouraged by local authorities, which not only satisfies the needs of the agar industry and abalone feed industry, but also contributes to improving water quality [11]. In addition, as seaweeds are efficient biofilters, the IMTA strategy with incorporation of seaweeds has been widely accepted and applied [23,56].

The seaweed *G. lemaneiformis* has proven to be an ideal biofilter and scrubber of nutrients. First, its life history is at least several months

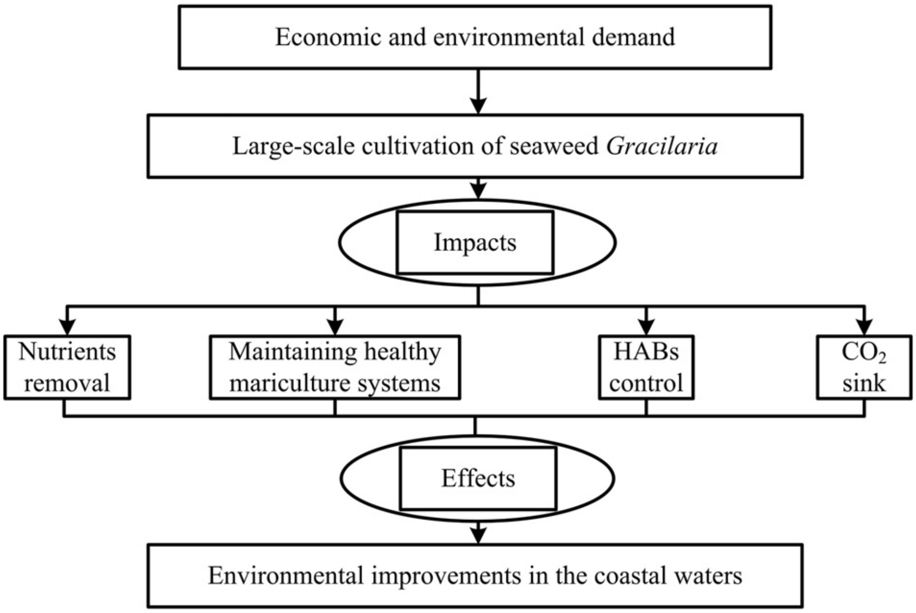

Fig. 4. Flowchart of the effect of *Gracilaria* cultivation on environmental improvements in the mariculture waters.

longer than that of microalgae. Second, harvesting *G. lemaneiformis* removes nutrients from coastal systems permanently, and its cultivation and harvest are relatively easy and less expensive compared to other seaweeds. The cultivation of *G. lemaneiformis* has proven to be an effective way for reducing environmental N and P loadings. In addition, this seaweed can out-compete HAB-forming species and decrease phytoplankton densities [12,24,64]. Finally, the floating-raft method is ideal to accommodate multiple ecologically-compatible species, such as fish, abalone, other seaweeds, and filter-feeding bivalves in ecosystems, making it a co-inhabit environment; the organisms co-cultured even mutually benefit each other. This kind of 'integrated mariculture' has self-cleaning capacity, provides environmentally friendly remediation of surrounding waters, and produces other valuable products, such as abalone [79]. Based on the current knowledge and available data, we develop a conceptual scheme to summarize *Gracilaria* cultivation development and its environmental improvement potential (Fig. 4).

Gracilaria species have been successfully cultivated and undergone rapid development in the coastal waters of China, which can be used as a very effective biofilter at industrial scales. They have become the most important seaweeds for integrated multi-trophic aquaculture systems and bioremediation engineering tools in the mariculture waters. The bioremediation with large-scale *Gracilaria* cultivation is promising in water quality improvement and harmful algae bloom control.

As eutrophication has become a worldwide environmental problem in many coastal areas, some countries have utilized seaweed cultivation as an important ecological strategy to improve water quality especially in mariculture waters [48,56,57]. It has been documented that cultivation of *Gracilaria* is environmentally beneficial in many Chinese coastal waters, which is established as a very good model for providing a new approach to coastal environmental improvement [11,12,23]. We firmly believe that the large-scale cultivation of seaweed holds the key to eco-friendly water quality improvement in the coastal waters of the world.

The environmental improvements by large-scale cultivation of seaweed are obvious, but it may produce some negative effects although few such studies have been conducted. First, large-scale cultivation may decrease the seawater exchange rate due to the huge biomass and long thalli (1–2 m) of *Gracilaria*. Second, because of fish grazing and extreme climate such as typhoon before harvest, some thalli of *Gracilaria* may break off and sink into the seafloor, and become new organic matter resource, possibly causing anoxia in bottom waters. Our recent study revealed a clear decreasing trend in sediment organic matter in a sediment core from the *Gracilaria* cultivation site of Nan'ao Island over the past decade, which is best explained by that seaweed harvest is indeed a removal of C from the coastal waters and potentially improves bottom-water DO levels. To better address the negative aspects of large-scale seaweed cultivation, future efforts such as long-term monitoring and enclosure experiments as currently implemented in the seaweed cultivation area, are greatly needed.

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