INTRODUCTION

Despite having surface areas amounting to only 7% of global ocean area and volumes amounting to <0.5% of total ocean volume, ocean coastal zones play an important role in the biogeochemical cycles of carbon. Significantly higher rates of new primary production occur in the coastal oceans than in the open oceans because of the higher supply of nutrients in coastal areas, in addition to the rapid remineralization of organic matter resulting from enhanced pelagic and benthic coupling (Wollast 1998, Muller-Karger et al. 2005). The scaling of air-sea CO2 fluxes based on measurements of the partial pressure of CO2 (pCO2) and carbon mass balance calculations indicates that the continental shelves absorb atmospheric CO2 at a rate ranging between 0.33 and 0.36 Pg C yr⁻¹. This corresponds to an additional sink of from 27 to 30% of the CO2 uptake by the open oceans (Takahashi et al. 2009). Unfortunately, even now there is still a great deal of discussion about whether coastal oceans are net sources or sinks of atmospheric CO2, and whether primary production in coastal oceans is exported or recycled. There is some evidence that estuaries act as sources of CO2 to the atmosphere due to the large fraction of terrestrial/riverine organic matter that is degraded and emitted as CO2 to the atmosphere (Chen & Borges 2009, Rabouille et al. 2001, Gazeau et al. 2004, Hopkinson & Smith 2005, Li et al. 2007). However, marine macrophytes (e.g. seagrasses and macroalgae) can also act as an effective carbon sink because of their large biomass and relatively long turnover time (1 yr) as compared to phytoplankton (1 wk; Smith & Mackenzie 1987). For example, in the Bay of Palma (Spain), a strong decrease in pCO2 over Posidonia meadows has been reported, and has been attributed to their higher primary productivity as compared to the surrounding oligotrophic waters (Gazeau et al. 2005). Giant kelp beds (Macrocystis pyrifera) have an influence on the diel cycles of pCO2 and dissolved inorganic carbon (DIC) in the sub-Antarctic coastal area (Delille et al. 2009). Without any added feed, seaweeds
and filter-feeding shellfish play an important role in the global carbon cycle.

China’s coastal ocean, extensive and rich in nutrients and resources, is a region with one of the highest productivity levels in the world (Tang 2006). Hu (1996) assessed the CO2 absorbing capacity of the East China Sea and stated that the East China Sea was ‘a weak carbon sink,’ taking up about 4.3 million t (Mt) C yr⁻¹. Tsunogai et al. (1996) considered the East China Sea as a net carbon sink area, which could absorb about 30.0 Mt C yr⁻¹. However, this conclusion did not include the shallower coastal waters, where there is high primary production. Along the coast of China, waters <15 m deep total some 124 000 km², about 4.1% of the total Chinese coastal ocean. Because natural primary production is high, and mariculture is a major activity in these waters, the oceanic carbon cycle of the area is highly active, seaweeds transforming DIC into organic carbon by photosynthesis, and filtering shellfish absorbing particulate organic carbon (POC) by feeding activity. Through the calcification process, a significant quantity of carbon can be imbedded into the shells of bivalves as CaCO₃. A considerable mass of carbon can therefore be removed from the ocean through harvesting. This removal process will have a significant influence on the carbon cycle in both the mariculture area and adjacent areas. Therefore, study of the contribution of shellfish and seaweed mariculture to the ocean carbon cycle will help in understanding the capacity of the coastal ecosystem to take up CO₂, thereby enhancing our understanding of the global carbon cycle.

MARICULTURE IN CHINA

Mariculture in China is highly developed, with both the extent of the cultured area and the annual production volume being relatively high and increasing. Food and Agriculture Organization (FAO) data show that in 1955 the total annual production of Chinese mariculture was only some 0.1 Mt, but that it has increased steadily over subsequent decades. From about 1990 the industry expanded dramatically, with output rising from ~1.6 Mt in 1990 to ~13.1 Mt by 2007, by which time it represented ~2/3 of total world mariculture production (FAO, www.fao.org). This major expansion was largely driven by new shellfish and seaweed mariculture in the shallow coastal waters. For example, in 2007, annual production of shellfish and seaweeds represented 77 and 10%, respectively, of total mariculture production in China, while shrimp and fish production represented 7 and 5%, respectively, and other species <1%.

Shellfish mariculture, in particular, began to expand rapidly in China in the early 1970s, and government data show that shellfish production has increased continuously and substantially since, rising from ~0.3 Mt in the early 1980s to ~1.0 Mt in the early 1990s and then to 9.9 Mt in 2007 (Fig. 1). The main species cultured are oyster, clam, scallop and mussel, their yields representing almost 78% of total Chinese mariculture production.

In the early stages of mariculture development, seaweeds (e.g. Laminaria and laver) were the dominant species in China. Since the 1990s, that sector of the industry has expanded rapidly, so that by 2002 the annual production of seaweed represented 20% of the total world output. In 2007, total production of seaweed in China reached 1.4 Mt (half-dry weight, which is equal to ~1.2 Mt dry weight), amongst which Laminaria, laver and others represented 57.2, 6.7 and 36.1%, respectively.

EFFECT OF MARICULTURE ON CARBON BUDGET

Seaweed

Recently, as a result of further research on the nutrient metabolism of seaweeds (e.g. carbon metabolism; Rivkin 1990, Flynn 1991, Gao & Mckinley 1994, Yang et al. 2005), the role of seaweed in the materials cycle of coastal ecosystems has become better understood. Seaweeds can transform DIC into organic carbon by photosynthesis, which can decrease the pCO₂ in seawater. Dissolved nutrients such as nitrate and phosphate can be taken up during photosynthesis to raise the alkalinity of surface water, which will further reduce seawater pCO₂ and therefore improve the rate at which atmospheric CO₂ diffuses into the seawater. Large-scale seaweed mariculture has become the most important primary producer in Chinese coastal ecosys-
tems because coastal seawater provides significant volumes of trophic materials. For example, in Sungo Bay of the Yellow Sea, the annual carbon production of seaweeds (Laminaria, sea lettuce, etc.) amounted to 9750 t, which represented 37% of the bay's total primary production. The annual carbon products of different benthic macrophytes ranged from 153 to 2664 g m\(^{-2}\), which is 7.5 times that of phytoplankton (Mao et al. 1993).

In different areas, many factors—including nutrients, temperature, and illumination—vary, causing differences in N and P levels in seaweeds and in primary production. However, there is usually no significant difference in the ratio of C to the total dry weight from different areas (Rivkin 1990, Flynn 1991). Usually, inorganic carbon is not the limiting factor for the growth of seaweed, while N, P or Si are limiting.

Table 1 lists the nutrient composition of a number of seaweeds. The ratio of carbon dry weight ranges from 20 to 35%, with significant differences between species. For example, the content of carbon in Laminaria is 31.2%, higher than in some other seaweed species (Rivkin 1990, Mao et al. 1993). Summing the yields of cultivated seaweeds and multiplying by the species-specific carbon content, in 2007 ∼0.34 Mt C were removed from the coastal ocean of China by harvesting.

Shellfish

Shellfish utilize carbon in 2 ways: (1) They use dissolved HCO\(_3\)– from seawater to generate calcium carbonate (CaCO\(_3\)) shells after Ca\(^{2+}\) + 2HCO\(_3\)– = CaCO\(_3\) + CO\(_2\) + H\(_2\)O (Chauvaud et al. 2003). The generation of 1 mol of CaCO\(_3\) releases 1 mol of CO\(_2\) into seawater. The release of CO\(_2\) from surface ocean water owing to precipitation of CaCO\(_3\) depends not only on water temperature and atmospheric CO\(_2\) concentration, but also on the CaCO\(_3\) and organic carbon masses formed (Lerman & Mackenzie 2005). In a strongly autotrophic ecosystem, CO\(_2\) production by carbonate precipitation may be counteracted by organic productivity through uptake of generated CO\(_2\), resulting in a lower transfer of CO\(_2\) from water to the atmosphere or even in a transfer in the opposite direction.

(2) Shellfish utilize oceanic carbon when feeding. Shellfish have a very effective filter-feeding system combined with a high filtration rate, which can withdraw phytoplankton and particulate organic materials from whole embayments. In a large-scale shellfish mariculture area, this filter-feeding activity can strongly affect the biomass of phytoplankton and the amount and composition of particulate organic carbon (POC) (Prins et al. 1995, Nakamura & Kerciku 2000, Zhang & Fang 2006). For example, in Sungo Bay, the filtration rates of mainly cultured scallop Chlamys farreri were very high, about 18.8 and 40.8% of stock POC were utilized by the scallop in April and May, respectively (Zhang & Fang 2006).

Table 2 shows the carbon content of shell and soft tissue of cultivated shellfish (Zhou et al. 2002), and Table 3 shows the weight proportions shellfish harvested at Sungo Bay. From each of the 4 species 20 individuals were sampled at random. Total wet weights (±0.1 g) were recorded. Dry soft tissue and shell weights were determined after drying at 60°C for 48 h. The data show soft tissue to contain ~44% C by dry weight (DW), and the shell only 12% C by DW. Differences of C content in shellfish among different geographical areas and different species were not significant. The main source of variation of the C:H:N ratio among different geographical areas and species was caused by variation in N content (Hawkins & Bayne 1985, Goulletquer 1989, Grant & Granford 1991, Zhou et al. 2002). Based on the annual yields in 2007 and on the data in Tables 3 and 4, an estimated 0.88 Mt C

<table>
<thead>
<tr>
<th>Common name</th>
<th>Species</th>
<th>Chemical composition (% DW)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laminaria</td>
<td>Laminaria japonica</td>
<td>31.2 1.63 0.379</td>
<td>Zhou et al. (2002)</td>
</tr>
<tr>
<td>Green laver</td>
<td>Ulva pertusa</td>
<td>30.7 1.87 0.392</td>
<td>Zhou et al. (2002)</td>
</tr>
<tr>
<td>Laminaria</td>
<td>Laminaria longicruris</td>
<td>28.77 1.40</td>
<td>Chapman et al. (1978)</td>
</tr>
<tr>
<td>Laminaria</td>
<td>Laminaria saccharina</td>
<td>23.36 2.26</td>
<td>Ahn et al. (1998)</td>
</tr>
<tr>
<td>Bull kelp</td>
<td>Nereocystis ulekeana</td>
<td>23.64 1.86</td>
<td>Ahn et al. (1998)</td>
</tr>
<tr>
<td>Laminaria</td>
<td>Laminaria groenlandica</td>
<td>28.7 1.83</td>
<td>Harrison et al. (1986)</td>
</tr>
<tr>
<td>Purple laver*</td>
<td>Porphyra yeoensis</td>
<td>27.39</td>
<td></td>
</tr>
<tr>
<td>Sea lettuce</td>
<td>Ulva lactuca</td>
<td>23.5 0.88 0.14</td>
<td>Lapointe et al. (1992)</td>
</tr>
<tr>
<td>Gracilaria</td>
<td>Gracilaria tikvahiae</td>
<td>28.4 2.23 0.04</td>
<td>Lapointe et al. (1992)</td>
</tr>
<tr>
<td>Gracilaria</td>
<td>Gracilaria ferox</td>
<td>20.6 1.52 0.07</td>
<td>Lapointe et al. (1992)</td>
</tr>
<tr>
<td>Brown alga</td>
<td>Fucus distichus</td>
<td>35.0 1.81</td>
<td>Rosenberg &amp; Probyn (1984)</td>
</tr>
</tbody>
</table>

*Carbon ratio calculated from the average value of seaweeds in the table.
were removed from the seawater by harvest, including 0.67 Mt C in shells (see Table 4).

Based on the energy budget $C = F + U + R + G$, where $C$ = total energy of ingestion, $F$ = feces energy, $U$ = excretion energy, $R$ = respiration energy, and $G$ = growth energy, the POC actually utilized by shellfish was equal to $C$, and the production of shellfish was approximately equal to $G$ (Karfoot 1987). Under different conditions, the $G:C$ ratios are different, ranging from 6.13 to 90.97% (Table 5). Considering the production of the different shellfish examined in this paper, we calculate that there were about 3.52 Mt POC taken up by cultured shellfish, including the 0.88 Mt C removed from the ocean by harvesting. Some was released into seawater in the form of CO$_2$ by respiration processes, and some POC formed bio-deposits through feces as part of the biogeochemical cycle, a process that accelerates the sedimentation of particles.

The long-line method is the main shellfish and seaweed mariculture method practiced in China. In such culture areas, fouling organisms usually become one of the most dominant populations. Because it is difficult to calculate the biomass of fouling, the results reported have excluded C contributed by fouling organisms. But measured at the cultivation equipment, the biomass of fouling is very large (Huang & Cai 1984), and includes a number of species. Most fouling organisms belong to filter-feeding species that also ingest suspended organic particles, and some of these species, such as barnacles and mussels, have calcareous shells. For example, in Sungo Bay the dominant fouling species was *Ciona intestinalis*, which, in August 2001, amounted to about 1600 g m$^{-2}$ (wet weight), with a total average number of individuals for each lantern net of about 800 (Zhang et al. 2005). Based on the extent of total cultured area and number of cages, it was estimated that the total number of *C. intestinalis* individuals was about $1.6 \times 10^{10}$. The DW composition was about 33.19% C (Zhou et al. 2002), making the average DW per individual ~0.055 g. Accordingly, we can calculate that the net production of C in Sungo Bay by *C. intestinalis* was nearly 320 t, which is ~6.4% of total C production by cultured scallops. Therefore, the effect of biofouling on the C cycle in shallow water cannot be ignored. The normal way of removing biofouling organisms today is changing the lantern nets. It must be concluded from these findings that the actual C utilized and removed by shellfish culture must exceed previously referenced estimates.

### DISCUSSION AND CONCLUSION

The above analysis demonstrates that the effect of shellfish and seaweed mariculture on the carbon cycle in coastal ocean waters is significant. As shown in Fig. 1, mariculture in the coastal ocean waters of China has become a large-scale activity, with production in 1999 close to 10 Mt. The latest 5-year average annual
production figures exceed 13 Mt. The annual production of shellfish and seaweed mariculture has increased year by year. Clearly, in such a large-scale production process a great deal of oceanic carbon is taken up, indirectly or directly, with some of it removed from the ocean. From 1999 to 2008, through the activity of shellfish and seaweed mariculture, 3.79 ± 0.37 Mt C yr⁻¹ (totaling 37.89 Mt C over the period) were utilized, while at least 1.20 ± 0.11 Mt C yr⁻¹ (totaling 12.04 Mt C) were being removed from the coastal ecosystems by harvesting (0.86 ± 0.086 Mt C yr⁻¹ by shellfish and 0.34 ± 0.029 Mt C yr⁻¹ by seaweeds), as shown in Tables 6 and 7. Most important was that 0.67 ± 0.061 Mt C yr⁻¹ were sequestered in shells. The above results also demonstrate that cultured shellfish and seaweed play important roles as a carbon sink, even as a carbon removal sink, in Chinese coastal waters. As we know, terrestrial ecosystems play a significant role in carbon absorption and storage (Fang et al. 2001, Piao et al. 2009). However, the effect of forest and vegetation in terrestrial ecosystems on the carbon cycle is short-term, since the carbon will later be released to the atmosphere by decomposition. In contrast, the effect of mariculture production on the carbon cycle is much more long-term. For example, shell carbon requires considerable time to return to the atmosphere. Cultivated shells removed from the ocean are in fact a long-term carbon removal sink, playing a significant role in carbon capture and storage. Large volumes of carbon utilized by cultivated shellfish and seaweeds are removed from coastal ocean waters by harvesting, and are not returned until they are consumed. Most of the shellfish and seaweeds in China are used in the production of food, animal feed, chemicals, cosmetics and pharmaceutical products. It is therefore worthwhile to develop an environmentally friendly mariculture, that not only provides high quality and safe seafood for human beings, but also contributes significantly to improving the capacity of coastal ecosystems to absorb atmospheric CO₂.

Our results show that a significant and quantifiable amount of carbon is removed from coastal ocean areas through the harvest of cultured shellfish and seaweed, yet the oceanic carbon biogeochemical cycling generated by mariculture activity is a process that remains not fully understood. For example, the key process of cultured shellfish acting as a marine bio-pump in the shallow sea plays an indirect role in the oceanic uptake of CO₂, which is the process of reducing the surface concentration of CO₂ and thus promoting the transfer of atmospheric CO₂ into seawater. But only if the fixed carbon capacity in coastal marine ecosystems results in a sufficient decrease in the concentration of surface CO₂ then the marine bio-pump can absorb atmospheric CO₂. There are several studies on the assessment of carrying capacity in mariculture (Fang et al. 1996a,b, Tang 1996, Duarte et al. 2003, Zhang et al. 2009), but little of this research has touched on the carbon cycle. Some research has demonstrated that macroalgal photosynthesis tends to increase surface oceanic pH (Pearson et al. 1998, Menendez et al. 2001), countering the tendency for pH to decline as bicarbonate becomes

### Table 5. Estimates of ratio of growth energy (G) in total energy income (C) of cultivated shellfish

<table>
<thead>
<tr>
<th>Shellfish (common name, species)</th>
<th>Experimental parameters</th>
<th>G/C × 100%</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chinese scallop Chlamys farreri</td>
<td>Shell height (mm)</td>
<td></td>
<td>Wang et al. (1999)</td>
</tr>
<tr>
<td></td>
<td>25.6</td>
<td>19.82</td>
<td></td>
</tr>
<tr>
<td></td>
<td>40.3</td>
<td>16.55</td>
<td></td>
</tr>
<tr>
<td></td>
<td>65.7</td>
<td>14.19</td>
<td></td>
</tr>
<tr>
<td>Manila clam Ruditapes philippinarum</td>
<td>Temperature (°C)</td>
<td></td>
<td>Zhang et al. (2002)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>6.13</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>26.82</td>
<td></td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>34.63</td>
<td></td>
</tr>
<tr>
<td>Green mussel Perna viridis</td>
<td>Season (month)</td>
<td></td>
<td>Wong &amp; Cheung (2001)</td>
</tr>
<tr>
<td></td>
<td>February</td>
<td>6.87</td>
<td></td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>45.84</td>
<td></td>
</tr>
<tr>
<td></td>
<td>July</td>
<td>52.43</td>
<td></td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>90.97</td>
<td></td>
</tr>
<tr>
<td>Bay mussel Mytilus trossulus</td>
<td>Quality and quantity of food:</td>
<td></td>
<td>Arifin et al. (2001)</td>
</tr>
<tr>
<td></td>
<td>Algae only</td>
<td>36.85</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Algae + silt (3:1)</td>
<td>55.69</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Algae + silt (1:1)</td>
<td>57.64</td>
<td></td>
</tr>
</tbody>
</table>

Tang et al.: Mariculture increases coastal ecosystem CO₂ absorption
carbonate in the process of shell calcification. Furthermore, research on the mechanisms of interaction among nutrients, phytoplankton, seaweeds and cultured shellfish is limited. Recent results indicate that shellfish transform small particles into larger fecal and pseudofecal matter through the filtration process, thus increasing the sedimentation rate of particulate materials (Navarro & Thompon 1997, Giles & Pilditch 2006, Mallet et al. 2006). In July 2002, in Sungo Bay, we found that the sedimentation rate of suspended particles in the mariculture area was 1.75 times that of the non-cultured area (Cai et al. 2003). In the spring, the assimilation rate of Chinese scallops was about 76%, and approximately ¼ of the C filtered from the water column was deposited as feces. Therefore, every day, there were 8 t POC being moved from the water column to the seabed by the physiological activity of the cultured scallop population, clearly an accelerated vertical transfer of C. So for any region with long-term, large-scale shellfish culture, significant volumes of bio-deposits will be generated. Due to the shallow water in cultured areas, the effect of winds and waves on resuspension of bio-deposits can significantly influence carbon flux rates in these areas. Research on the effects of wind-induced mixing of coastal waters on biogeochemical flux is limited and superficial. Our results indicate that it is important to obtain a better understanding of carbon biogeochemical cycling related to large-scale culture of shellfish and seaweed in coastal waters, as well as the role of shellfish and seaweed mariculture in the carbon cycle and in healthy and sustainable development of coastal ecosystems.

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