Responses of summer phytoplankton community to drastic environmental changes in the Changjiang (Yangtze River) estuary during the past 50 years

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ABSTRACT

The phytoplankton community in the Changjiang Estuary is subject to intensive physical and chemical stresses because of human- and climate-driven changes. We obtained historical data on summer phytoplankton communities from 1959 to 2009 to explore responses to long-term environmental changes. The nitrogen (N) and phosphorus (P) concentrations and ratios (N/P and N/Si) increased because of persistent riverine loading, but silicon (Si) levels remained constant. Climatic changes and extensive water diversions and withdrawals (sediment retention) resulted in a series of physical alterations, including increased temperature, turbidity reduction, and river plume shrinkage. These changes induced a dramatic increase in microalgal biomass (cell density and chlorophyll a) with a decreasing diatom-dinoflagellate ratio, and exacerbated harmful algal blooms. In the past dominant net-collected species were usually chain-forming diatoms; however, more recently, large dinoflagellates and filamentous cyanobacteria dominate. This was not consistent with information from water samples (co-dominated by small dinoflagellates), because of the loss of solitary species collected using a 76-μm net. The dominant species shifted from temperate-subtropical/eurythermal to subtropical-tropical/eurythermal taxa in the warmer water caused by global warming and hydrographic changes. There was also an increased dominance of euryhaline/high-salinity species due to increase in Kuroshio transport and the northward Taiwan Warm Current and reduction in Changjiang Diluted Water. All these changes in phytoplankton communities appear to be closely related to an increase in anthropogenic activities and climatic changes.

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1. Introduction

Marine phytoplankton is a major contributor to global primary production, and its community structure is carefully monitored by oceanographers, because it is crucial to ecosystem structure and function (Hays et al., 2005). Rapid increases in population and economic activity in the last 50 years has promoted eutrophication of coastal and estuarine waters though a massive influx of nutrients and other biogenic elements (Anderson et al., 2002; Li et al., 2007a). A large body of literature (Anderson et al., 2002; Hays et al., 2005; Zhou et al., 2008) has demonstrated large variation in microalgal assemblage composition [e.g. biomass increase, diatom-dinoflagellate ratio alteration, and frequent harmful algal blooms (HABs)] around the world, due to anthropogenic eutrophication and climatic changes. These variations induce a succession of ecological and socioeconomic impacts on coastal waters (Hays et al., 2005).

Delta-front estuaries of large rivers are important interfaces between continents and the oceans. They experience material fluxes that have a global impact on marine biogeochemistry, and preserve a record of natural and anthropogenic environmental changes (bianchi and allison, 2009). The Changjiang (Yangzte River) Estuary (CE), one of the most important estuaries located in the East China Sea (ECS), western North Pacific, is subject to strong human activities and climatic changes. Since the 1980s, ever-expanding population and economic aggregation in the Changjiang Basin led to drastic increases in nutrient (N and P) fluxes into the CE (Li et al., 2007a; Chai et al., 2009; Jiang et al., 2010; Dai et al., 2011; Gao et al., 2012), and ultimately resulted in nutrient over-enrichment and ratio (N/P and Si/N) alteration. This pressure exacerbated HABs in terms of frequency, range, persistence, and destructive capability, especially in warm months (Zhou et al., 2008; Wang and Wu, 2009; Liu et al., 2011). The recent sharp reduction in runoff and sediment (Dai et al., 2011; Yang et al., 2007; Wang et al., 2013b), as well as hydrographical alteration (e.g. mixed layer depth and circulation patterns) (Lee et al., 2004; Yan et al., 2008) of the CE due to large-scale water diversions and withdrawals (e.g. >50000 dams), including the Three Gorges Dam (TGD) impoundment in 2003, may severely affect the microalgal composition, distribution, and HAB occurrence (Chen et al., 2003; Gong et al., 2006; Jiao et al., 2007; Miller et al., 2008; Roelke and Pierce, 2011).

Global warming induced a sea surface temperature (SST) rise in the ECS (Tang et al., 2009; Wang et al., 2013a), especially in the CE (belkin, 2009). Climatological forcing, abnormal/extreme weather (chan and liu, 2004) and climate fluctuation in the western North Pacific influenced the East Asian monsoon (kimoto, 2005), river plume extension, oceanic circulation paths and strength (Kimoto, 2005; Sakamoto et al., 2005), and vertical stratification (doney et al., 2012) through the ocean–atmosphere interaction, and caused a visible alteration in the physical environment in the ECS (belkin, 2009; Tang et al., 2009). These changes were responsible for varied circulations and water masses, including the Changjiang Diluted Waters (CDW), Taiwan Warm Current (TWC), Coastal Current, and the Kuroshio. Phytoplankton is particularly sensitive to such disturbances (Hays et al., 2005). Under increased global/regional climatic changes and anthropogenic activities, phytoplankton in the CE was subject to intensive physicochemical stresses, and its community variation associated with the environmental changes was of considerable concern to researchers. However, long-term changes in phytoplankton communities in response to large multiple environmental perturbations remain poorly documented. Available reports (Wang, 2006; Li et al., 2007a, 2007b; Zhou et al., 2008; Chai et al., 2009; Jiang et al., 2010; Dai et al., 2011) almost entirely focus on anthropogenic eutrophication effects on the phytoplankton community, and rarely referred other stress factors (e.g. SST increase, sediment, runoff, and hydrographic variations) under increasing human activities and climate changes.

Since 1959, a large number of phytoplankton studies in the CE (Guo and yang, 1992; Wu et al., 2004; He and Sun, 2009) have been performed using plankton nets with 76-μm mesh. Early phytoplankton samples in the CE were almost all collected using this type of net because of the Chinese specifications for marine monitoring, and until recently few collections were conducted using water sampling (Juan et al., 2006; Li et al., 2007b). In summer, significant physical–chemical processes occur in the ECS, which highlight the effect of regional/global changes on phytoplankton assemblage. Thus, this work concentrated on summer (June–September) net- and water-collected phytoplankton associated with physical–chemical forcing in the CE from 1959 to 2009. Our objective was to explore long-term changes in summer phytoplankton communities in relation to environmental factors in the CE under extensive human activities and climate changes. We examined changes in the biomass, dominant species, diatom-dinoflagellate composition, and community diversity as well as the HABs involving the putative physicochemical stresses (e.g. recent river plume shrinkage associated with decreased runoff, turbidity reduction, SST increase, circulation alteration, and nutrient over-enrichment), that have not been documented comprehensively in previous studies.

2. Material and methods

2.1. Study area

The Changjiang which flows into the ECS (Fig. 1) is the third longest (6300 km) and fifth largest river in terms of discharge volume (~900 km³ y⁻¹) in the world, with a catchment area of about 1.8 × 10⁶ km². The river catchment has the East Asian monsoonal climate, which results in higher rainfall in summer and lower in winter. The maximum runoff occurs from May to October (i.e. during the wet season), contributing 71.8% of the annual flow recorded at Datong station (Yu and Shen, 2011). The CE receives huge amounts of freshwater, sediment, and nutrient input from the Changjiang, especially in summer.

2.2. Data source

We collected historical data recorded since 1959 on phytoplankton abundance, chlorophyll a (Chla), diatom-dinoflagellate composition, dominant species, Shannon
diversity ($H'$), and Pielou evenness ($J'$) indices. We also compiled data on HABs and nutrients [dissolved inorganic nitrogen (DIN: $NO_3^- + NO_2^- + NH_4^+$), dissolved reactive phosphorus (DRP), and dissolved silicate (DSi)] in both freshwater (salinity $< 0.5$) and saline sections of the CE (Tables S1–S5). Also, we examined the outflow volume and sediment input from the Changjiang recorded at Datong station. The annual runoff showed little variation with an average of $2.8 \times 10^4$ m$^3$ s$^{-1}$ from 1959 to 2009, while the sediment discharge and concentration decreased significantly during this time (Table 1 and Fig. S1). Runoff decreased in the wet season and increased in the dry season, especially the percentages of runoff for the two seasons, which show significant (MK test, $Z = \pm 2.26$, $p < 0.05$) trends (Table S7 and Fig. S2). During 1998–2009, wet and dry season runoff decreased (Fig. S2), however on the wet season decrease was significant (MK test, $Z = -2.81$, $p < 0.01$).

3.1. Environmental factors

3.1.1. Runoff and sediment from Changjiang

The summer maximum runoff occurred in the 1990s, and the minimum in the 2000s (Fig. 2A). However, both the sediment concentration (Fig. 2B) and influx (Fig. 2C) decreased as recorded by the Datong station. The annual runoff showed little variation with an average of $2.8 \times 10^4$ m$^3$ s$^{-1}$ from 1959 to 2009, while the sediment discharge and concentration decreased significantly during this time (Table 1 and Fig. S1). Runoff decreased in the wet season and increased in the dry season, especially the percentages of runoff for the two seasons, which show significant (MK test, $Z = \pm 2.26$, $p < 0.05$) trends (Table S7 and Fig. S2). During 1998–2009, wet and dry season runoff decreased (Fig. S2), however on the wet season decrease was significant (MK test, $Z = -2.81$, $p < 0.01$).

3.1.2. Temperature

Summer SST in the CE increased significantly ($p < 0.001$) from 1982 to 2009 (by 1.31 °C with a rate of 0.49 °C/decade, according to Sen’s estimation) (Fig. 3 and Table 1). In August, the SST increased at a rate of 0.66 °C/decade.

Because of a low level of anthropogenic activities [e.g. nutrient levels and runoff remained fairly constant (Duan et al., 2007; Li et al., 2007a)] in the Changjiang Basin. The summer AVHRR SST in the CE (29.5–33.0 N, 122.0–125.0 E) from 1982 to 2009 was obtained from the Pathfinder v5 dataset (http://www.ncdc.noaa.gov/oa/climate/research/sst/oil-daily-information.php).

The dataset contains daily gridded AVHRR SST data with approximately 4 km spatial resolution and is described more fully in Kilpatrick et al. (2011).
3.1.3. Nutrient load
The NO₃ ($p < 0.001$) and DRP ($p < 0.05$) concentrations in the freshwater section of the CE increased significantly (Fig. 4 and Table 1), while DSi varied slightly ($p > 0.05$). Consequently, the NO₃/DRP increased moderately, while the DSi/NO₃ decreased dramatically. However, after the TGD impoundment, the DSi level decreased gradually from 2004 to 2010 (MK test, $S = -11$, $p < 0.05$; Table S7). The nutrient concentrations and ratios in the saline section show similar trends (Fig. 5 and Table 1).

![Table 1 - Results of the Mann-Kendall test for detection of long-term trends in the environmental and phytoplankton data in summer.](image)

<table>
<thead>
<tr>
<th>Parameters</th>
<th>$Z$</th>
<th>$p$</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yearly runoff</td>
<td>0.13</td>
<td>&gt;0.05</td>
<td>51</td>
</tr>
<tr>
<td>Yearly sediment discharge</td>
<td>-5.93</td>
<td>&lt;0.001</td>
<td>51</td>
</tr>
<tr>
<td>Yearly sediment concentration</td>
<td>-6.38</td>
<td>&lt;0.001</td>
<td>51</td>
</tr>
<tr>
<td>Sea surface temperature</td>
<td>3.58</td>
<td>&lt;0.001</td>
<td>28</td>
</tr>
<tr>
<td>NO₃ in freshwater section</td>
<td>4.55</td>
<td>&lt;0.001</td>
<td>19</td>
</tr>
<tr>
<td>DRP in freshwater section</td>
<td>2.59</td>
<td>&lt;0.05</td>
<td>18</td>
</tr>
<tr>
<td>DSi in freshwater section</td>
<td>1.28</td>
<td>&gt;0.05</td>
<td>17</td>
</tr>
<tr>
<td>NO₃/DRP in freshwater section</td>
<td>0.53</td>
<td>&gt;0.05</td>
<td>18</td>
</tr>
<tr>
<td>DSi/NO₃ in freshwater section</td>
<td>-4.00</td>
<td>&lt;0.001</td>
<td>17</td>
</tr>
<tr>
<td>DIN in saline section</td>
<td>1.53</td>
<td>&gt;0.05</td>
<td>13</td>
</tr>
<tr>
<td>DRP in saline section</td>
<td>2.38</td>
<td>&lt;0.05</td>
<td>13</td>
</tr>
<tr>
<td>DSi in saline section</td>
<td>0.62</td>
<td>&gt;0.05</td>
<td>12</td>
</tr>
<tr>
<td>DIN/DRP in saline section</td>
<td>1.03</td>
<td>&gt;0.05</td>
<td>12</td>
</tr>
<tr>
<td>DSi/DIN in saline section</td>
<td>-1.44</td>
<td>&gt;0.05</td>
<td>12</td>
</tr>
<tr>
<td>Net-phytoplankton abundance</td>
<td>0.79</td>
<td>&gt;0.05</td>
<td>15</td>
</tr>
<tr>
<td>Average surface chl a</td>
<td>2.86</td>
<td>&lt;0.01</td>
<td>10</td>
</tr>
<tr>
<td>Surface chl a maximum</td>
<td>1.98</td>
<td>&lt;0.05</td>
<td>15</td>
</tr>
<tr>
<td>Dominance of Skeletonema spp.</td>
<td>-2.16</td>
<td>&lt;0.05</td>
<td>16</td>
</tr>
</tbody>
</table>

3.2. Phytoplankton community

3.2.1. Biomass (abundance and Chla) increase
Net-collected phytoplankton abundance increased ($p > 0.05$) in the CE, despite high variation in the dataset from 1959 to 2009 (Fig. 6A and Table 1). The water-collected phytoplankton density also increased (Fig. 6B). Summer average (Fig. 6C) and maximum (Fig. 6D) surface Chla increased significantly ($p < 0.05$) from the 1980s.

![Fig. 3 - Changes in summer sea surface temperature (SST) in the CE (29.5–33.0°N, 122.0–125.0°E) from 1982 to 2009.](image)

![Fig. 4 - Changes in summer nutrient concentrations and ratios in the freshwater section in the CE (data source are shown in Table S4).](image)

3.2.2. Diatom and dinoflagellate composition
The proportions of dinoflagellate density and species number in the phytoplankton community in the CE increased dramatically, while the net- and water-collected diatoms gradually declined (Fig. 7). Both the net- (Fig. 7D) and water-collected (Fig. 7E) total species number increased gradually.

3.2.3. Dominant species shift
The dominant species found in the net-collected phytoplankton samples consisted of chain-forming diatoms (e.g.
genus *Skeletonema*, *Pseudo-nitzschia*, *Chaetoceros*, *Proboscia*, and *Rhizosolenia*. Recently, large dinoflagellates (e.g. *Ceratium* spp. and *Noctiluca scintillans*) and filamentous cyanobacteria (i.e. *Trichodesmium thiebautii*) dominated in the CE (Table 2). However, water-collected samples were dominated by colonial diatoms and small dinoflagellates (e.g. *Prorocentrum donghaiense* and *Scrippsiella trochoidea*). The dominant species shifted from temperate-subtropical/eurythermal to subtropical-tropical/eurythermal taxa (e.g. *T. thiebautii*, *Chaetoceros pseudocurvisetus*, and *Proboscia alata f. gracillima*). Similarly, the dominance of the euryhaline/high-salinity species enhanced as well. The dominance of *Skeletonema* spp. decreased significantly (Fig. 8 and Table 1).

3.2.4. Community diversity

The $H'$ and $J'$ indices of the net-collected phytoplankton community around the river mouth (31.0–32.0°N, 121.0–122.5°E) increased slightly, while the water sample indices off the mouth (30.5–32.0°N, 122.0–123.5°E) increased obviously since 2002 (Fig. 9).

3.3. Harmful algal blooms

HAB occurrence increased rapidly (Fig. 10). Moreover, the HAB species changed from mainly *Skeletonema* spp. and *N. scintillans* to various taxonomic compositions, including diatoms, dinoflagellates, chlorophytes, and *Phaeocystis* (Table S8). In particular, *P. donghaiense* bloomed most frequently since 2000 (>50% of the total frequency), although the HABs caused by *Skeletonema* spp. also increased dramatically.

4. Discussion

River discharge decreased in the 2000s, especially in the wet season during 1998–2009 (Fig. S2). At the same time, the precipitation increased slightly and evaporation decreased (Wang et al., 2011; 2013b). The decrease in river discharge may be attributed to the recent increase in dams, reservoirs and water diversion in the Changjiang Basin (Xu et al., 2010). Extensive water conservancy projects trapped massive amount of sediment and reduced the sediment concentration (Fig. 2B) and flux (Fig. 2C). Yang et al. (2007) calculated that the sediment inflow into the estuary decreased by 31%, because the sediment was retained by the TGD after it began operation in 2003–2005. Consequently, turbidity was reduced and light penetration enhanced thus promoting primary production in the CE (Chen et al., 2003), as phytoplankton in this turbid estuary suffers from severe light limitation. For example, after the TGD impoundment in June 2003, the sharp reduction in river outflow was followed by an algal biomass (Chla) increase near the river mouth (Jiao et al., 2007). Furthermore, the first stages of the eastern and middle routes of China’s South-to-North Water Diversion are already under construction and will be completed in 2013 and 2014 with water diversion of 8.9 and 9.5 × 10^9 m^3, respectively. This reduction in runoff will profoundly influence the algal community in the CE via a series of physicochemical (e.g. salinity, nutrient availability, stratification, and hydraulic flushing) alterations (Miller et al., 2008; Roelke and Pierce, 2011). Therefore, we should pay more attention to the effects of this large water conservancy project on the estuarine ecosystem.

As a result of global warming and transport strengthening of TWC (due to enhanced Kuroshio) (Tang et al., 2009), summer SST in the CE increased significantly from 1982 to 2009 (Fig. 3). For example SST in August increased at a rate of 0.66°C/decade. This finding agreed well with SST elevation in the northern ECS (Tang et al., 2009; Wu et al., 2013; Wang et al., 2013a). Belkin (2009) found accelerated warming of the CE from 1982 to 2003, at a rate of up to 1.0°C/decade. This upward
trend was confirmed by measured atmospheric (Wu et al., 2011) and seawater temperature (Wang et al., 2013a) at the Shengshan station (30.8°/C14E, 123.0°/C14E; located at the CE), recorded from 1985 to 2005 and 1985–1999, respectively. The shrinkage of CDW (due to recent significant reductions in wet season runoff; Fig. S2) combined with increasing TWC and Kuroshio extensions (Jiao et al., 2007) bring about more high-temperature and high-salinity phytoplankton species. Furthermore, increased salinity and SST promoted growth of different species which contributed to increased subtropical-

Fig. 6 – Changes in summer net- ($\times 10^4$ cells m$^{-3}$) and water-collected ($\times 10^4$ cells L$^{-1}$) phytoplankton abundance and chlorophyll a (Chls; $\mu$g L$^{-1}$) in the CE (data source are shown in Tables S1 and S2).

Fig. 7 – Summer (A, B, D, and F) net- and (C, E, and G) water-collected diatom–dinoflagellate composition in the CE (data source are shown in Table S1). BD: percentage (%) of Bacillariophyta density in total phytoplankton density; DD: percentage (%) of Dinophyta density in total phytoplankton density; TSN: total species number; BSN: percentage (%) of Bacillariophyta species number in TSN; DSN: percentage (%) of Dinophyta species number in TSN.
Table 2 – Long-term changes in dominant species of net- and (bold font) water-collected phytoplankton in the CE (data source are shown in Table S1).

<table>
<thead>
<tr>
<th>Time</th>
<th>Main dominant species</th>
<th>(dominance, %)</th>
</tr>
</thead>
<tbody>
<tr>
<td>07/1959</td>
<td>Skeletonema spp.** (89.1), Pseudo-nitzschia pungens** (5.9), Chaetoceros spp. (2.8)</td>
<td></td>
</tr>
<tr>
<td>08/1959</td>
<td>Skeletonema spp., P. pungens*, Chaetoceros spp.</td>
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<tr>
<td>07/0-0600</td>
<td>Skeletonema spp. (99.0)</td>
<td></td>
</tr>
<tr>
<td>08/1982</td>
<td>Skeletonema spp. (62.7), Thalassiosira subtillia** (35.4)</td>
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<tr>
<td>08/1985</td>
<td>Skeletonema spp. (99.0)</td>
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</tr>
<tr>
<td>06/0-0806</td>
<td>Skeletonema spp. (84.4)</td>
<td></td>
</tr>
<tr>
<td>08/1988</td>
<td>P. pungens (32.5), Eucampia zoodiacus** (27.7), Chaetoceros lorezenianus** (12.9), Skeletonema spp. (3.4)</td>
<td></td>
</tr>
<tr>
<td>08/1989</td>
<td>S. costatum (97.2)</td>
<td></td>
</tr>
<tr>
<td>07-08/1999</td>
<td>Chaetoceros pseudocurvisetus** (67.7), Proboscia alata f. gracillima* (15.5), C. lorezenianus (4.0)</td>
<td></td>
</tr>
<tr>
<td>08/2000</td>
<td>Skeletonema spp. (99.3)</td>
<td></td>
</tr>
<tr>
<td>07/2001</td>
<td>Skeletonema spp., Chaetoceros spp.</td>
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<td>08/2001</td>
<td>Skeletonema spp. (69.6), Coscinodiscus jonesianus* (21.8), Coscinodiscus oculus-iridis* (2.3)</td>
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<td>08/2002</td>
<td>Skeletonema spp. (66.1), P. pungens (11.8), Chaetoceros affinis* (6.5), C. lorezenianus (3.9)</td>
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<td>08/2003</td>
<td>Skeletonema spp. (39.2), Chaetoceros curvisetus* (19.8), Chaetoceros diadema* (17.6), C. lorezenianus (7.1)</td>
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<td>08/2004</td>
<td>Skeletonema spp., P. alata f. gracillima, C. lorezenianus</td>
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<td>Skeletonema spp. (74.2), C. curvisetus** (6.0), C. lorezenianus (5.4), P. pungens (3.0)</td>
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<td>06/2006</td>
<td>Skeletonema spp. (26.2), P. pungens (28.2), Chaetoceros debilis* (16.8), Rhizosolenia styloformis* (6.3)</td>
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<td>08/2006</td>
<td>Skeletonema spp. (67.2), P. alata f. gracillima (14.9), Thalassionema nitzschioides** (5.6), C. diadema** (4.6)</td>
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<td>08/2007</td>
<td>C. curvisetus (25.4), P. pungens (16.4), Skeletonema spp. (16.0), C. lorezenianus (12.6)</td>
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<td>06/2009</td>
<td>P. pungens (41.6), Ceratium tripos* (16.0), Skeletonema spp. (9.5), Coscinodiscus argus* (9.0), Noctiluca scintillans* (5.8), Pseudo-nitzschia delicatissima** (4.4)</td>
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<td>08/2009</td>
<td>P. pungens (10.4), Pseudo-nitzschia spp. (7.5), Chaetoceros compressus* (7.4), R. styloformis (7.0), C. lorezenianus (4.9), C. pseudocurvisetus** (4.6), Prorocentrum thibautii (3.9), Thalassiothrix frauenfeldii (3.9)</td>
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<td>08/2002</td>
<td>Skeletonema spp. (58.8), P. delatissimass, C. affinis**, C. curvisetus</td>
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<td>06/2003</td>
<td>Skeletonema spp. (67.1), Prorocentrum donghaiense** (20.5)</td>
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<td>08/2004</td>
<td>Skeletonema spp., Thalassiosira spp., Scripsiella trochoidea</td>
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<td>09/2005</td>
<td>Skeletonema spp. (95.4)</td>
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<td>P. donghaiense (45.8), Karenia mikimoto (26.4), P. pungens (5.6), P. delatissimass (6.2)</td>
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<td>T. nitzschioides (70.4), Skeletonema spp. (14.4), C. jonesian (3.8), C. fusus (4.5)</td>
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<td>08/2009</td>
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<tr>
<td>08/2009</td>
<td>Thalassiosira curviserata** (15.3), Skeletonema spp. (12.9), P. pungens (11.3), T. subtillia (7.4), Prorocentrum minimum** (4.6), R. styloformis (4.0)</td>
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| (a) Eurythermal species. | (b) Temperate species. | (c) Temperate-subtropical species. | (d) Subtropical-tropical species. |
and 5), the non-siliceous algae gradually became more dominant and influenced the CE phytoplankton assemblage composition by decreasing the diatom-dinoflagellate ratio in terms of cell density and species number (Fig. 7). In addition, the HAB species changed from multiple species (e.g. *Skeletonema* spp. and *N. scintillans*) in 1980s–1990s to a wider taxonomic composition, including diatoms, dinoflagellates, chlorophytes, and *Phaeocystis*, especially the species *P. donghaiense* bloomed most frequently (>50% of the total frequency) since 2000 (Table S8). These results are supported by paleoceanographic data. Jin et al. (2010) found an increasing production of non-siliceous algae with decreasing diatoms after 1980 in the CE, due to massive N and P inputs and nutrient ratio alteration. Also, Dai et al. (2012) demonstrated that dinoflagellate cyst density in the CE increased from the 1980s. Although the dominant net-collected species still consisted of chain-forming diatoms, large dinoflagellates and filamentous cyanobacteria increased more recently (Table 2). This finding is not consistent with water-sample data, due to the easy loss of non-colonial small cell size dinoflagellates (e.g. *P. donghaiense* and *S. trochoidea*) when collected with a 76-µm net. The CE is likely to continue toward Si limitation of diatom growth and primary production dominated by non-siliceous algae.

The increase in cell density and species richness of dinoflagellates was partly responsible for physical changes in the CE. Increasing summer solar irradiance lead to steady thermocline and halocline regimes, the bottom strong northward TWC (cold and heavy water) and upper CDW (warm and light water) (Su and Yuan, 2005). Accelerated warming (Belkin, 2009), increasing Kuroshio transport and a southerly TWC (Kimoto, 2005; Tang et al., 2009) intensified the vertical stratification and caused nutrient-rich stratified water columns (Doney et al., 2012) in the ECS, which favoured dinoflagellates (Sellner et al., 2001). Burkholder et al. (2008) reported that mixotrophic HAB species thrived in eutrophic habitats, which respond directly to nutrient inputs, and indirectly through high-density bacterial and algal prey. The recently dominant dinoflagellates (e.g. *Ceratium tripos*, *P. donghaiense*, and *S. trochoidea*) in the CE, mostly as the mixotrophy (Jeong et al., 2010), benefited from relatively high nutrients, irradiances, terrigenous organic matter, and food sources (Troost et al., 2005). Therefore, the dinoflagellate dominance increased gradually in the CE. Furthermore, path variations in ocean current and strengthening circulation may play an important role in the planktonic community composition. With river plume reduction (Lee et al., 2004; Gong et al., 2006), TWC and Kuroshio transport enhancement (Tang et al., 2009), and summer SST elevation (Fig. 3), offshore water intrudes inshore on the ECS shelf further carrying with it abundant warm-water dinoflagellates, which result in increasing dinoflagellate domination. This explanation differs from previous studies (Li et al., 2007a, 2007b; Zhou et al., 2008; Jiang et al., 2010), which only considered nutrient factors.

*Skeletonema* spp. are generally considered to be the most important population in the CE, because they dominate the community (Table 2) and have frequently (up to 30% of the total frequency) induced HABs since 1980 (Table S2). However, their domination decreased significantly in recent data (Fig. 8). This change may be caused by nutrient ratio alteration, runoff

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**Fig. 8** Changes in dominance of (A) net- and (B) water-collected *Skeletonema* spp. in the CE (data from Table 2).

**Fig. 9** Changes in Shannon diversity (*H’*) and Pielou evenness (*J’*) indices of (A) net- and (B) water-collected phytoplankton community in the CE (data source are shown in Table S3).
reduction, and temperature and salinity increases. Firstly, as a diatom species, Skeletonema spp. growth was inevitably inhibited by the sharp decline in Si/N which reduced its competitive advantage over other planktonic populations. Secondly, this microalgal population generally dominated (>95% in total cell density) and bloomed at the principal part of CDW plume where the salinity was lower than 23 (Guo and Yang, 1992; Wu et al., 2004). Runoff reduction and offshore water intrusion increased the salinity of the river mouth and decreased dominance and spatial distribution of this species in the CE. Finally, their optimal growth temperature is about 25 °C in the CE (Guo and Yang, 1992), so the observed temperature increases during July–September (Fig. 3) which exceed this value are harmful to this population. However, the reduced domination of Skeletonema spp. increased the phytoplankton H’ and J’ (Fig. 9). Additionally, the enhanced TWC and Kuroshio transport carried abundant offshore species which amplified the species diversity and richness (Figs. 7 and 9) in the CE.

5. Conclusions

The present work confirmed that long-term changes in the phytoplankton community in the CE were closely related to physical–chemical variations (e.g. eutrophication, extensive riverine water diversions and withdrawals, SST increase, and hydrographic alteration) caused by human activities and climatic changes. However, a quantitative relationship is difficult to determine because of the lack of time-series data and the complex interactions in the system. The consequences of shifts in phytoplankton communities and their connections with observed changes in zooplankton, benthic, and fish communities are unknown. More attention should be paid to future potential adverse changes in phytoplankton communities. The CE is a major estuary that records natural and anthropogenic environmental variations, and thereby contributes to further understanding the responses of estuarine phytoplankton communities to global/regional changes. This study will be useful to local and international environmental managers because most global estuaries are suffering from extensive human and climate-driven changes.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.watres.2014.01.032.

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