

Decadal variations in diatoms and dinoflagellates on the inner shelf of the East China Sea, China*

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Abstract Diatoms and dinoflagellates are two major groups of phytoplankton that flourish in the oceans, particularly in coastal zone and upwelling systems, and their contrasting production have been reported in several world seas. However, this information is not available in the coastal East China Sea (ECS). Thus, to investigate and compare the decadal trends in diatoms and dinoflagellates, a sediment core, 47-cm long, was collected from the coastal zone of the ECS. Sediment chlorophyll-*a* (Chl-*a*), phytoplankton-group specific pigment signatures of diatoms and dinoflagellates, and diatom valve concentrations were determined. The sediment core covered the period from 1961 to 2011 AD. The chlorophyll-*a* contents ranged from 2.32 to 73 $\mu\text{g/g}$ dry sediment (dw) and averaged 9.81 $\mu\text{g/g}$ dw. Diatom absolute abundance ranged from 29 152 to 177 501 valve/gram (v/g) dw and averaged 72 137 v/g dw. Diatom valve and diatom specific pigment marker concentrations were not significantly correlated. Peridinin increased after the 1980s in line with intensified use of fertilizer and related increases in nutrient inputs into the marine environment. The increased occurrence of dinoflagellate dominance after the 1980s can be mostly explained by the increase in nutrients. However, the contribution of dinoflagellates to total phytoplankton production (Chl-*a*) decreased during the final decade of this study, probably because of the overwhelming increase in diatom production that corresponded with the construction of the Three Gorges Dam (TGD) and related light availability. Similarly, the mean ratio of fucoxanthin/peridinin for the period from 1982 to 2001 was 6% less than for 1961 to 1982, while the ratio for 2001 to 2011 was 45.3% greater than for 1982 to 2001. The decadal variation in the fucoxanthin/peridinin ratio implies that dinoflagellate production had been gradually increasing until 2001. We suggest that the observed changes can be explained by anthropogenic impacts, such as nutrient loading and dam construction.

Keyword: anthropogenic impact; benthic diatoms; pigment signature; nutrient concentration; Three Gorges Dam construction

1 INTRODUCTION

Diatoms and dinoflagellates dominate phytoplankton in coastal and upwelling areas of the ocean, and play a variety of roles in ecosystems (Klais et al., 2011; Hinder et al., 2012). These two phytoplankton groups exhibit unique, distinct, and often contrasting adaptive ecologies, enabling them to maintain their niche partitioning worldwide despite

the turbulence-nutrient matrix of habitats and onshore-offshore gradients (Smayda, 2002). In marine systems, the water column thermo-physical dynamics

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are intrinsically associated with the production and distribution of pelagic and benthic populations, which in turn are strongly coupled with the distribution of algal remains in marine sediments (Jones and Birks, 2004). Consequently, the relationship between the algal remains and the water column physico-chemical condition has provided a strong basis for using algal remains as biological indicators of changes in algal production and environmental conditions. Thus, sediment-preserved remains, such as phytoplankton pigment, and skeletal structures, such as diatom frustules, provide a useful basis for biogeochemical studies, and can be used to gain an improved understanding of long-term plankton abundance and compositional changes (Battarbee et al., 2002; Finkelstein and Gajewski, 2007; Schüller and Savage, 2011).

The East China Sea (ECS) is a marginal sea; it is considered one of the most dynamic sea systems in the world because of the range of eutrophic conditions and environmental changes it experiences (Huh and Su, 1999; Su and Huh, 2002; Zhou et al., 2008). In recent years, changes have been reported in biological production and phytoplankton species composition in several coastal water systems and seas in response to long-term changes in climate (Sugimoto and Tadokoro, 1997; Chiba and Saino, 2003; Leterme et al. 2005; Zhang and Gong, 2005; Kuwae et al., 2006; Beaugrand, 2009; Montes-Hugo et al., 2009; Klais et al., 2011; Hinder et al. 2012). Similarly, Zhou et al. (2008) reported a decreasing trend in the contribution of diatoms to the entire phytoplankton community in the Changjiang (Yangtze) River estuary (CRE) and adjacent coastal ECS since the 1960s. The area that entails the Changjiang River Basin and the coastal region of the ECS is well-known for its intensive industrial and agricultural activities and numerous densely populated urban areas. These activities have contributed to ongoing increases in fertilizer use and disposal of waste materials that ultimately find their way into the CRE and the ECS. Consequently, increasing trends in dissolved nitrogen, phosphorus, and chlorophyll-*a* (Chl-*a*) (Chai et al., 2006) concentrations; increased frequency of red tides (Zhou et al., 2008); decreases in dissolved silica; and changes in the composition of bloom forming-phytoplankton (Li et al., 2007) have been recorded in the estuary and adjacent coastal areas of the ECS over the past five decades.

Just as nutrients loads have changed in response to increases in artificial fertilizer use, sediment loads are

subject to substantial changes because of dam construction (Song et al., 2008; Wang et al., 2011). However, there is a lack of scientifically robust information about the responses of diatoms and dinoflagellates to changes in nutrients, sediment, and sediment-related conditions in the coastal zone of the ECS, from either long-term sampling or sediment cores. The aim of this study therefore was to bridge this knowledge gap by 1) analysing the long-term variation in total phytoplankton production, 2) analysing the long-term variations in diatom and dinoflagellate production using phytoplankton-group specific marker pigments, and 3) comparing diatom production using the diatom valve count and pigment signature as proxies. To achieve these aims, a sediment core sample was collected from the coastal zone of the ECS and long-term changes in diatom and dinoflagellate production were investigated and compared.

2 MATERIAL AND METHOD

2.1 Study area

The East China Sea is the largest continental marginal sea in the Western North Pacific (Huh and Su, 1999; Chiang et al., 2004) and is one of the most developed shelf areas in the world. Primary production on its wide shallow continental shelf is supported by frequent replenishment of nutrients to the euphotic zone from a deeper layer (Furuya et al., 2003). Vast quantities of terrigenous and anthropogenic materials flow into the ECS from different river basins and, as a result, it supports high biological production (Furuya et al., 2003). Our study site was located at 28°26.159 1'N and 122°11.074 5'E, close to the CRE, in the inner shelf area of the ECS. The sampling area was characterized by fine-grained sediments, dispersed from the Changjiang's plume (McKee et al., 1983). Cheng et al. (2014) reported that centric diatoms and one species of silicoflagellate (*Dictyocha fibula*) were the dominant species in the area from the CRE to the ECS.

Sedimentation rates in the ECS vary considerably and have been estimated to be between ~0.02 and 2 cm/a, with sedimentation decreasing towards the south along the inner shelf and towards the east in an offshore direction (Huh and Su, 1999). The ECS borders mainland China, the Kuroshio Current (KC), Taiwan and the Taiwan Strait, and the Yellow Sea to the west, east, south, and north, respectively (Huh and Su, 1999) (Fig.1). During the winter season, the majority of the runoff from the Changjiang River

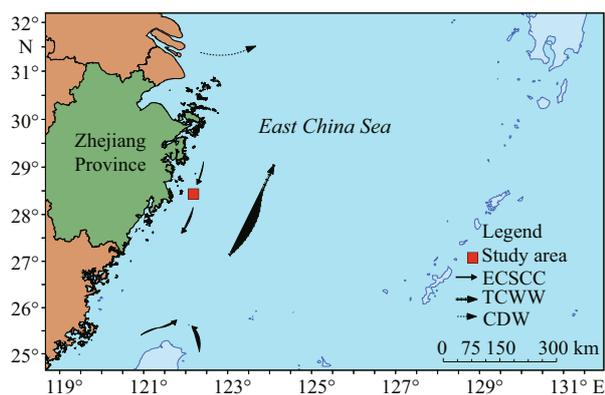


Fig.1 Location of the study area showing the sampling site (red), and regional water circulation and current regimes, including the Changjiang River Diluted Water (CDW), the East China Sea Coastal Current (ECSCC), and the Taiwan Current Warm Water (TCWW)

flows southeastward along the coast of Zhejiang Province. During the summer season, the increased runoff from the Changjiang River turns eastward or northeastward towards Cheju Island, Korea (Zhou et al., 2008). The ECS is a dynamic system that results from the interactions of different currents. The warm and oligotrophic KC and the Taiwan Warm Current (TWC), both with high temperatures and salinities (Huh and Su, 1999), dominate the circulation and flow northward along the edge of the ECS shelf. The Changjiang Cold Water (CJCW) has low salinity and temperatures and flows southward along the bottom of the coast of mainland China (Milliman et al., 1989). Because of these major currents, the ECS experiences high tidal currents, extremely high sediment loads, frequent and intense storm events, and consequent re-suspension of sediments. These physical features and processes ensure that the ECS is one of the most dynamic marginal seas in the world (Huh and Su, 1999).

2.2 Sediment processing and dating

A sediment core sample, 47-cm long, was collected at a water depth of 43 m from 28°26.159 1'N and 122°11.074 5'E. After collection, the sediment core was sliced into 2-cm intervals and approximately 0.5 cm of the outer rim of each sediment slice was trimmed off to minimize contamination between layers. Sediment samples were then placed in a freezer at -20°C until laboratory analysis. Sediments were dated with the α -spectrometry ^{210}Pb (via ^{210}Po) method (Huh and Su, 1999; Su and Huh, 2002), and ^{210}Pb dates were calculated using the method outlined by Appleby and Oldfield (1978). Semi-log plots were

used to derive ^{210}Pb -based deposition rates. From the slope (m) of the exponential downcore decrease in ^{210}Pb (decay), and assuming a constant initial radionuclide concentration (despite variable sedimentation rates), sediment accumulation rates (SPb^{-210}) were calculated using $\text{SPb}^{-210} = -\lambda/m$, where λ was the decay constant of ^{210}Pb .

2.3 Pigment and diatom valve analyses

Sediment samples were processed in a dark room. Homogeneously mixed freeze-dried sub-samples (about 5 g) were transferred into 50-mL centrifuge tubes and covered with aluminium foil to prevent light exposure. The pigments were then extracted with 10 mL of N,N-dimethyl ammonium naphthalene acetic acid (DMF) by shaking for 2 h at 100 r/min on a rotating mixer (Scieniz HS-3). Extracts were centrifuged (3 000 r/min, 15 min) and filtered through a 0.2- μm GF/F membrane (Whatman). Extracted filtrates (approximately 600 μL) were poured into HPLC tubes and mixed with ammonium acetate (1 mol/L) at a volume ratio of 1:1. All pigments were quantitatively analyzed by Daa HPLC (Ultimate 3000, Thermo Fisher). For chromatographic separation, samples of approximately 100 μL were injected through a C8 column (Agilent, Germany) for reverse phase chromatography using 1 mol/L ammonium acetate and methanol (20:80 v), and 100% methanol. Pigments were then identified and calibrated according to their peak patterns and retention times (Zapatal et al., 2000; Romero-Viana et al., 2009). The dry weight of the sediment was also determined and wet concentrations were converted to dry weight, and the pigment concentration per gram of dry weight ($\mu\text{g/g dw}$) calculated. Some pigments were selected as biomarker signatures; for example, chlorophyll-*a*, peridinin, fucoxanthin, and diatoxanthin and diadinoxanthin were chosen as indicator pigments for total phytoplankton production, dinoflagellates, diatoms, and for both dinoflagellates and diatoms, respectively (Higgins and Mackey, 2000; Verleyen et al., 2004; Schüller and Savage, 2011; Aneeshkumar and Sujatha, 2012). Since the relative abundance of specific carotenoid pigments was selectively affected during deposition, pigments were examined individually relative to historical down-core maxima and minima (Leavitt, 1993).

Prior to the sediment diatom analysis, wet sediment (1 g) was weighed and HCl and H_2O_2 were added to remove carbonates and organic matter (Renberg, 1990). To identify diatom species and count valves,

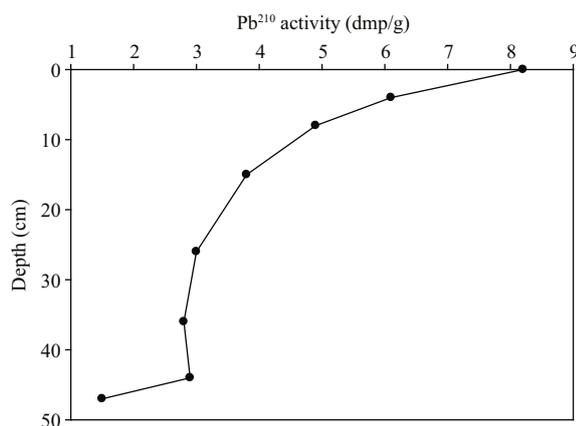


Fig.2 Core profile of excess Pb²¹⁰ concentrations for the age model

well-mixed acid-treated sediment suspensions containing diatom valves were mounted on microscope slides using Naphrax. Prepared slides were observed under a fluorescence microscope (Olympus BX51TRF) at magnifications of 400 or 1 000. Subsamples from the top, middle, and bottom of the sediment core were observed under a scanning electron microscope (JSM6390). Broken valves were counted using the method of Schrader and Gersonde (1978). The dry weight of the sediment was also determined and the wet valve count was converted to dry weight, following which the number of diatom valves per gram of dry weight (v/g dw) was then calculated. Taxa were identified to species and sub-species level using appropriate identification keys (Guo and Qian, 1984; Jin et al., 1985, 1992; Round et al., 1990; Cheng et al., 2012a; 2013).

2.4 Statistics and software applications

The Shannon diversity index was used as a measure of diatom species diversity and was calculated using a multivariate statistical package (MVSP 3.2). We categorized the diatoms and pigment ratios into their closest groups (time periods, in this case) to facilitate comparison of long-term changes using TWINSPAN 2.3 (two-way indicator for species analysis (Hill et al., 1975; Hill and Šmilauer, 2005)). Biostratigraphic analysis was carried out with C2 (version 1.7.5). The relative production of planktonic diatoms relative to total diatom abundance (planktonic diatom:total diatom abundance; Plan:Tabn) was calculated. To show decadal variations in diatom assemblage, the percentile compositions of dominant diatom species were analysed. Dominant species were defined as those that contributed more than 3% and occurred in

more than 3 different subsamples.

The ratio of accessory pigments to Chl-*a* has been used previously as a more conservative proxy to calculate the contribution of different groups of algae (Goericke and Montoya, 1998 and references therein). We calculated the ratios between different pigment signatures to highlight the decadal variation in diatom and dinoflagellate occurrences. The fucoxanthin/TChl-*a* (fuc/TChl-*a*) ratio was calculated to estimate relative diatom production; to ensure there was no bias from dinoflagellates, diatoxanthin and diadinoxanthin, these were not incorporated in the equation. The ratio of fucoxanthin/peridinin (fuc/per) was calculated to support calculation of decadal trends in ecological interactions between diatoms and dinoflagellates. Since water column irradiance and physico-chemical variables are intrinsically associated with phytoplankton species composition and their pigment composition, we calculated the relative production of planktonic diatoms relative to the total diatom abundance (planktonic diatom:total diatom abundance; Plan:Tabn). The irradiance conditions are also considered important for diatoms. We calculated the diatom mean irradiance by adding diadinoxanthin (DD) and diatoxanthin (D) concentrations and dividing by total chlorophyll-*a* (TChl-*a* is the sum of chlorophyll-*a* and its derivatives and bacteriochlorophylls) (Verleyen et al., 2004).

3 RESULT

3.1 Sediment age

Results from ²¹⁰Pb dating of the sediment core showed that the average sedimentation rate was 0.94 cm²/a, which shows that each centimetre represents about one year's sediment accumulation. The excess ²¹⁰Pb, calculated by subtracting the ²²⁶Ra activity from the total ²¹⁰Pb activity, is illustrated in Fig.2. Based on the calculated sedimentation rate, the 47-cm-long sediment core is about 50 years old, and covers the period from 1961 to 2011 AD. The core showed no evidence that sediments had been either reworked or disturbed by burrowing or fragments of animal remains. Furthermore, the inverse relationship between ²¹⁰Pb activity and core depth shows that the sediment was not substantially mixed or reworked. Considering the dynamic character of the ECS, Su and Huh (2002) and Huh and Su (1999) suggested that ²¹⁰Pb profiles should be supported by other sediment profiles such as ¹³⁷Cs and ^{239,240}Pu. Comparison of the results from this study agreed well with sedimentation

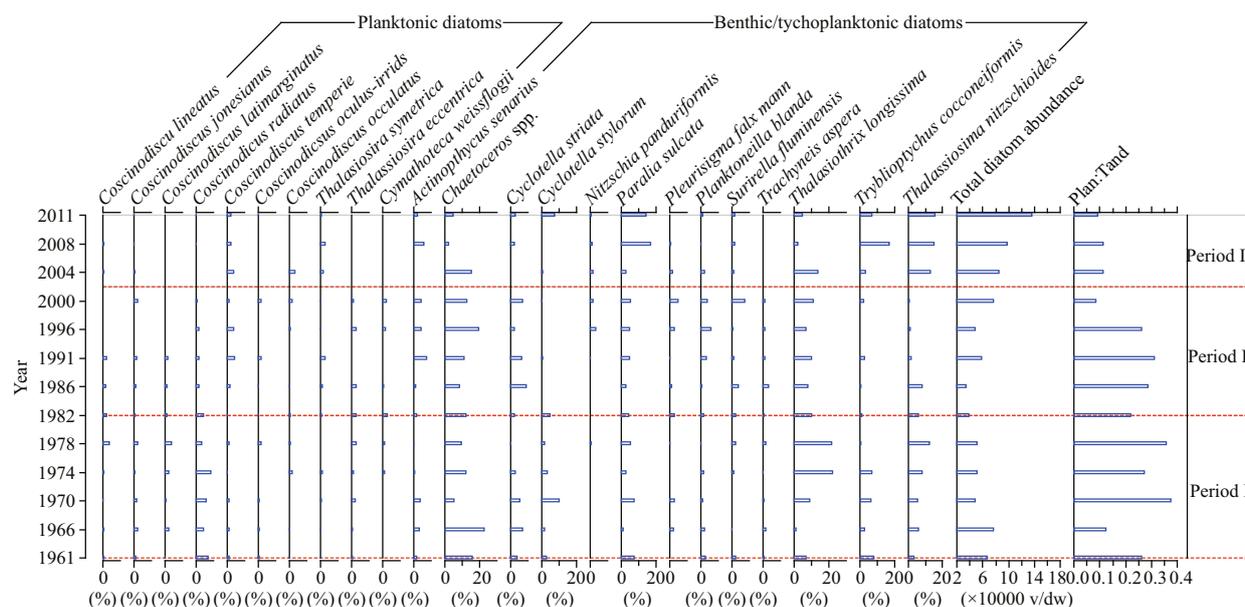


Fig.3 Decadal variations in diatom species composition, total diatom absolute abundance, and the ratio of planktonic diatom:total diatom abundance (Plan:Tabn)

rates of between 0.6 to 0.9 cm/a calculated by Su and Huh (2002) and Huh and Su (1999) from ^{137}Cs and $^{239,240}\text{Pu}$ sediment profiles of the inner shelf of ECS, close to our study area. Recently, Cheng et al. (2014) reported an average sedimentation rate of 1.57 cm/a. The difference between the sedimentation rates for the two studies reflects the characteristics of the study sites; that is, the study area of Cheng et al. (2014) was situated close to the coastal area of the CRE, which receives more sediments from the Changjiang River.

3.2 Diatom abundance and species composition

The results from TWINSpan 2.3 analysis show that the time span of the sediment core was divided into three periods, namely period I from 1961 to 1982, period II from 1982 to 2001, and period III from 2001 to 2011. A total of 135 diatom taxa belonging to 37 genera were identified, and 23% of the species were from the centric diatom genus *Coscinodiscus*. After *Coscinodiscus*, the three pennate diatom genera, *Pleurosigma*, *Trachyneis*, and *Nitzschia*, contributed 8%, 7%, and 6%, respectively. Diatom absolute abundance varied with depth and ranged from 29 152 to 177 501 v/g dw and averaged 72 137 v/g dw (Fig.3). Generally, the concentrations of sediment diatom valves were moderate. The Shannon species diversity index ranged from 2.917 to 3.413 and averaged 3.22, and species richness varied from 43 to 75 species. Benthic diatom species were dominated by species such as *Actinopterychus senarius*, *Planktoneilla blanda*, *Thalassiothrix longissima*, *Thalassionema*

nitzschioides, and *Trybliopterychus cocconeiformis*.

Diatom abundance increased after 2001, which coincides with the TGD construction in 2003. There was a clear pattern in the decadal values of the planktonic diatom:total diatom abundance ratio (Plan:Tabn ratio); in general, the planktonic diatom species abundance increased and dominated from 1961 to 2001, whereas benthic diatoms dominated from 2001 to 2011 (Fig.3). The mean values of the Plan:Tabn ratio were 0.25, 0.27, and 1.6 for periods III, II, and I, respectively.

3.3 Long-term trends in pigment concentrations

Chl-*a* was the main pigment in the sediment core followed by pheophorbide-*a*. With the exception of pheophorbide-*a*, the lowest and highest mean concentrations of all pigments were recorded in period I and period III, respectively (Fig.4). In period I the concentrations of fucoxanthin and peridinin were relatively low. The concentration of all pigments increased noticeably in period III, with maximum values observed between 2001 and 2007. The changes in the decadal concentrations of pheophorbide-*a* in the three periods were minimal compared with the variation observed in other pigments, such as fucoxanthin, peridinin, diatoxanthin, and diadinoxanthin. Relative to the concentration in period I, the concentration of fucoxanthin increased by 48.7% in period II (1982–2001) and increased by 191% in period III relative to period II. Peridinin increased by only 34.9% and 51.5% in periods II and

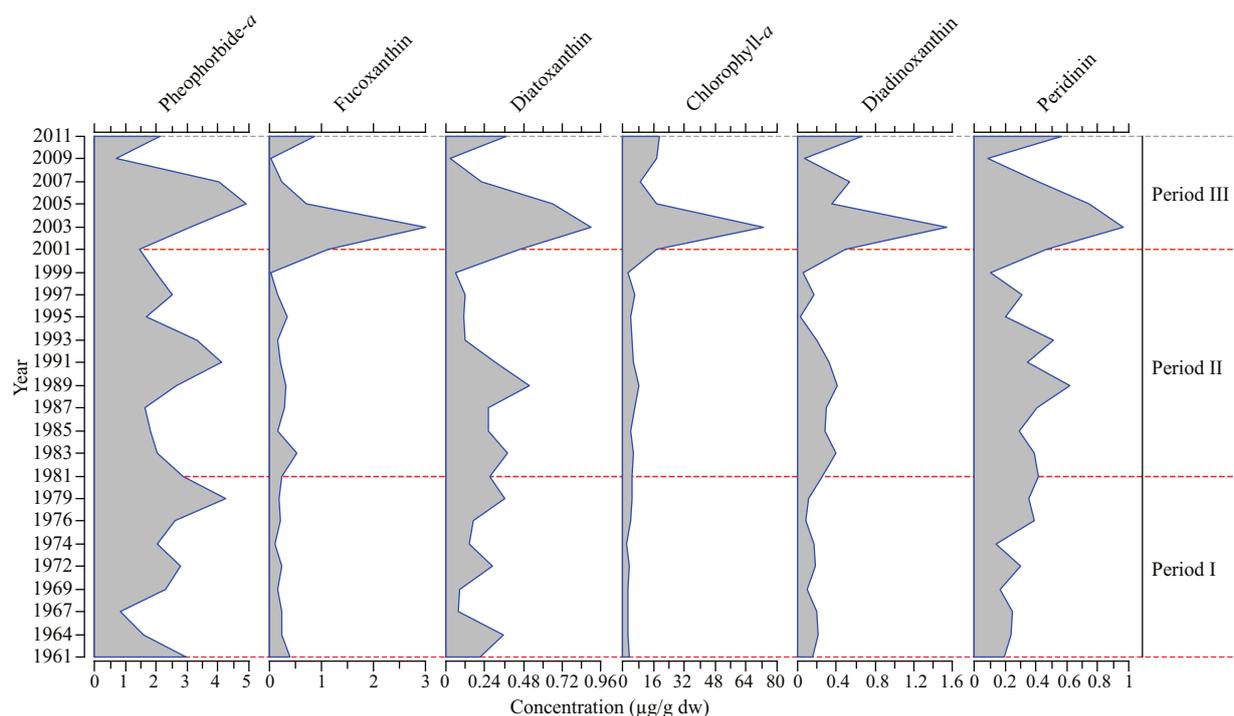


Fig.4 Decadal variations in pigment concentrations ($\mu\text{g/g}$) in period I (1961–1982), period II (1982–2001), and period III (2001–2011)

III relative to the concentrations in the preceding periods. The positive correlation between fucoxanthin and Chl-*a* ($R=0.94$, $P<0.05$) was stronger than that between peridinin and Chl-*a* ($R=0.71$, $P<0.05$). Diatom valve abundance was not correlated with diatom marker pigments.

3.4 Long-term variation in pigment ratios

The ratios of fucoxanthin/TChl-*a*, diatom mean irradiance (diatoxanthin+diadinoxanthin/TChl-*a*), and fucoxanthin/peridinin have gradually decreased over the past 50 years. Trends in the ratios also changed after 2001 (Fig.5). The fucoxanthin/TChl-*a* ratio gradually decreased until 2001 and then rapidly increased after 2001. The peridinin/TChl-*a* ratio increased from mid-1970 to mid-1980, decreased randomly until 2003, and then increased slightly from 2003 to 2007. The fucoxanthin/peridinin ratio was relatively low from 1961 to 2001 and then dramatically increased after 2001. The fucoxanthin/peridinin ratio decreased by 3.1% in period II relative to the ratio in period I, and increased by 45.3% in period III relative to the ratio in period II. There was no clear pattern in the diatom mean irradiance from 1961 until the late 1990s, after which it decreased noticeably. The ratio of TChl-*a*/fucoxanthin was 163.6% higher in period II than in period I and was 420% higher in period III

than in period II, and coincided with increases of 93.5% and 305.5% in the Chl-*a* concentration in periods II and III, respectively.

4 DISCUSSION

4.1 Phytoplankton production and preservation

The East China Sea is considered one of the most productive systems in the world (Gong et al., 2006). However, the observed moderate sediment pigment concentrations and the low diatom valve abundance indicate that phytoplankton remains were poorly preserved in sediments from the ECS. The concentrations of sediment-preserved signatures may be low because picoplankton are the major primary producers in the ECS and also account for the majority of surface water Chl-*a* (Yuh-Ling and Chen, 2000; Song et al., 2008). Generally, picoplankton are efficiently grazed by microzooplankton (Zhang et al., 2006), which results in the production of faecal pellets that are readily lost through photodegradation or reingestion (Welschmeyer and Lorenzen, 1985), or grazing of microzooplankton by mesozooplankton and incorporation into higher trophic biomass (Zhou et al., 2011) before being deposited into sediment. In line with this, Chl-*b* and other pigments mainly contributed by picophytoplankton species would not

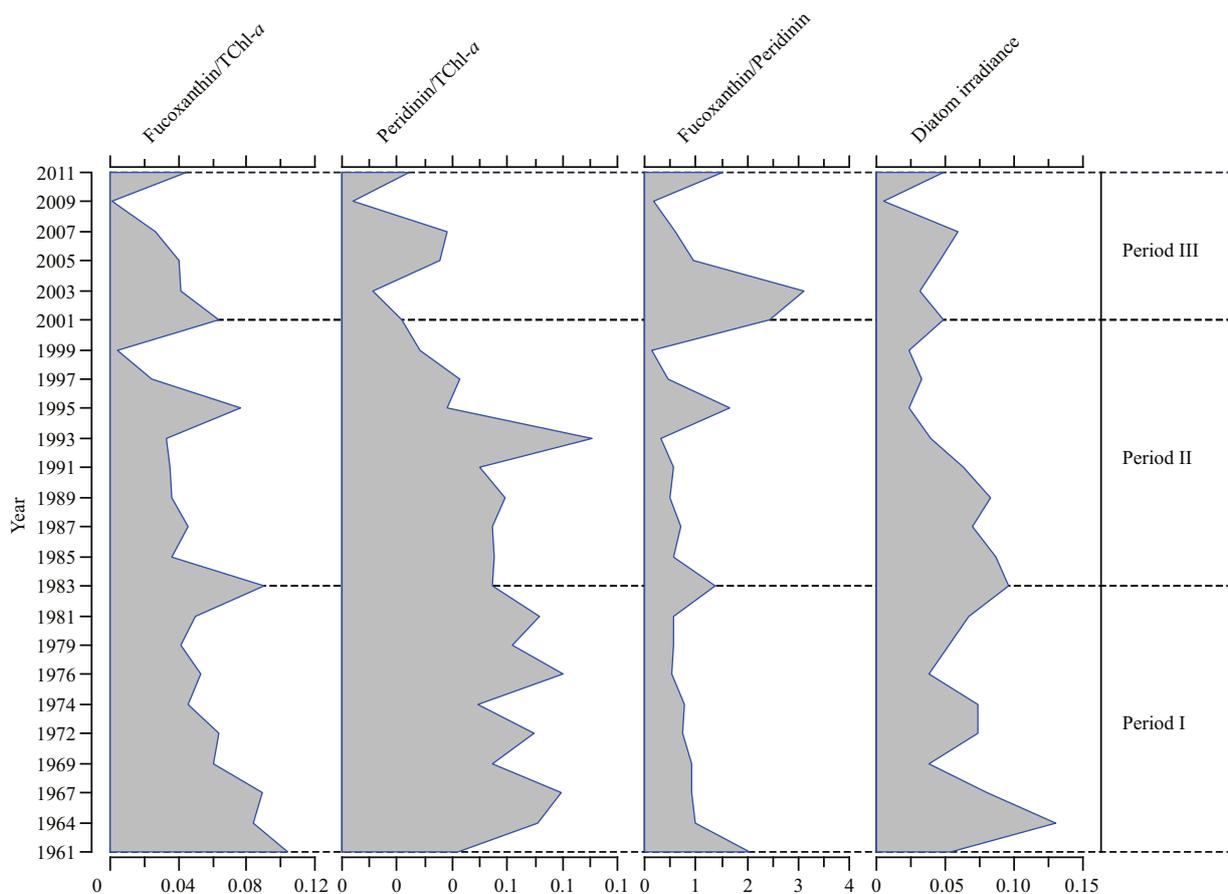


Fig.5 Decadal patterns in the relative production of diatoms (fucoxanthin/TChl-*a*), relative production of dinoflagellates (Peridinin/TChl-*a*), diatom production relative to dinoflagellate production (fucoxanthin/peridinin), and diatom mean irradiance (diatoxanthin+diadinoxanthin/ TChl-*a*, D+DD/TChl-*a*) in the three periods

be expected in the ECS. The low diatom valve concentrations may be the result of differential dissolution of weakly silicified species like *Skeletonema costatum* (Schüller and Savage, 2011) and current wash (Furuya et al., 2003). As the ECS is exposed to frequent mixing processes and has large shallow areas (Su and Huh, 2002), the phytoplankton remains spend more time in the water column, resulting in increased physico-chemical and biological degradation and loss of the phytoplankton remains. Furthermore, large amounts of terrestrial sediment discharged into the ECS by the Changjiang River (Furuya et al., 2003) dilute the proxy, leading to reduced concentrations of phytoplankton remains in the sediment.

The absence of any correlation between diatom valve counts and pigment markers indicates that there was a discrepancy between diatom production and the preservation of its remaining materials. The same result has been reported for Doubtful Sound, New Zealand (Schüller and Savage, 2011), where weakly silicified diatom species like *Skeletonema costatum*

disappeared because of selective dissolution, resulting in discrepancies between diatom abundance and pigment data. However, Verleyen et al. (2004) found a positive correlation between diatom pigments (diadinoxanthin, diatoxanthin, fucoxanthin) and diatom biovolume in the marine sediment. The general long-term trend in diatom marker pigments was comparable to the diatom valve abundance, except during period II, when the abundance of diatom valves decreased and pigment marker concentrations increased. This increase was probably related to diatom marker pigments contributed by other phytoplankton groups. Other researchers reported that there were no correlations between peridinin and dinoflagellate abundance (Leavetti and Findlay, 1994) or fucoxanthin and diatom abundance (Schüller and Savage, 2011) in lake and coastal sediments, respectively.

The Chl-*a* concentration indicates the presence of autotrophic benthic organisms, undegraded phytoplankton detrital material, and faecal pellets, and is well-accepted as an indicator of primary

production. In general, the decreases and increases in Chl-*a* coincided closely with increases and decreases in both peridinin and fucoxanthin. The strong positive correlations between Chl-*a* and both peridinin and fucoxanthin indicate the dominance and co-occurrence of these two phylogenetic groups (mainly diatoms and dinoflagellates) in the phytoplankton composition of the ECS. Some of the dinoflagellate groups may also contribute fucoxanthin. Hansen and Josefson (2003) reported a strong positive correlation between fucoxanthin and Chl-*a* in the transition zone of the North and Baltic Seas. The fact that the correlation between Chl-*a* and fucoxanthin was stronger than that between Chl-*a* and peridinin implies that diatoms are the dominant phytoplankton group and represent the greatest proportion of total phytoplankton production in the coastal ECS.

4.2 Temporal variation in diatom and dinoflagellate production

The changes in the fucoxanthin/peridinin ratio indicate that the relative productions of diatoms and dinoflagellates have changed. In particular, diatom production has been gradually decreasing in the past 50 years up to 2001. This decrease can be explained by regional climate fluctuations (Lin and Lu, 2009; Lee et al., 2012) and nutrient changes (Chai et al., 2006; Li et al., 2011) observed around the Changjiang River Basin and in the coastal ECS since the late 1970s. In the ECS, the general trend in Chl-*a* production indicates the influence of climate change and anthropogenic impacts and has been coupled with a major local-regional climate shift, the TGD construction, and anthropogenic nutrient inputs.

4.2.1 Period I

In this period, human influences on the ECS and its surroundings were not significant, and the western North Pacific regional climate was characterized by cool weather and decreased rainfall (Chai et al., 2006; Song et al., 2008; Lin and Lu, 2009; Haiyan et al., 2010; Wang et al., 2011; Lee et al., 2012). Data from this study indicate that diatom primary production was moderate in this period, which is consistent with the result recorded by Haiyan et al. (2010), who used BSi and Chl-*a* as proxies of paleo-productivity.

4.2.2 Period II

This period is recognized by a shift in the local-regional climate to warm and wet conditions (Lin and

Lu, 2009; Lee et al., 2012) and increased inputs of nitrogen-containing fertilizers (Chai et al., 2006; Li et al., 2011). Coincidentally, dinoflagellate production started to increase from the late 1970s. The fucoxanthin/peridinin ratio declined in this period, indicating that the increased production of dinoflagellates came at the expense of diatom production. The rise in dinoflagellate production was associated with the increase in artificial nitrogen inputs in the area surrounding the ECS, which shifted the balance of the N:P ratio in coastal systems. Considering the evolutionary advantages of dinoflagellates and their ability to bloom under nutrient-depleted conditions (Rivkin and Swift, 1985), the observed increase in dinoflagellate production over the past three decades is not unexpected. It is also consistent with previous studies of the ECS; for example, Kui (2007) reported a declining pattern in the contribution of diatoms to total phytoplankton abundance, with average contributions of 90%, 85%, and 64% in the early 1980s, mid-1980s, and in 1997, respectively. Shifts in the patterns of diatom and dinoflagellate dominance because of climatic variations have been reported from the central Baltic and the North Sea (Alheit et al., 2005) and elsewhere (deYoung et al., 2004; Wooster and Zhang, 2004). Leavetti and Findlay (1994) reported phytoplankton pigment compositional change because of nitrogen fertilization in an experimental lake, while Klais et al. (2011) also reported dissolved silica depletion that coincided with a significant increase in dinoflagellate abundance in the semi-enclosed Gulf of Riga.

Fucoxanthin, a pigment largely from diatoms and other phytoplankton, such as prymnesiophytes, crysophytes, and some dinoflagellates (Higgins and Mackey, 2000) showed a considerable (48.7%) increase during the period from 1982 to 2001. The rise of fucoxanthin in this period was probably associated with the increased production of dinoflagellates, as some dinoflagellate species contain this pigment (Jeffrey et al., 1997). This idea is supported by the fact that 1) peridinin made a considerable contribution to the total pigment concentration and peridinin was strongly correlated with fucoxanthin, and 2) other fucoxanthin-containing microalgae, such as crysophytes (19'-butanoyloxy-fucoxanthin) and prymnesiophyceae (19'-hex-fucoxanthin) (Higgins and Mackey, 2000), were absent from sediment samples. However, in contrast to the increased fucoxanthin concentrations observed

in this period, diatom valve abundance decreased in this period. Similarly, Haiyan et al. (2010) also reported decreased diatom production from 1980 to 1997. This therefore suggests that the increase in the Chl-*a* concentration during this period was the result of the increased production of dinoflagellates and other algal groups. In the same way, Haiyan et al. (2010) also suggested increases in the production of algae other than diatoms for the period from 1980 to 1997.

4.2.3 Period III

During this period, the pigment concentrations and diatom valve abundances increased drastically, which indicates that dinoflagellate, diatom, and total phytoplankton production increased noticeably after 2001. The highest pigment concentration was recorded between 2001 and 2007, and reflects the impact of the TGD construction. Furthermore, relative to the concentrations between 2004 and 2006, pigment concentrations decreased sharply between 2008 and 2010, but were still considerably higher than those recorded before construction of the TGD. This further indicates the pronounced impact of the TGD construction on the coastal zone of the ECS. The impact of the TGD construction is probably related to various complex physico-chemical and biological interactions. For example, the TGD construction reduced the volume of freshwater entering the ECS at least during water filling periods, which reduced stratification by density in the coastal ECS and promoted phytoplankton production. The TGD construction also resulted in a decrease in the terrestrial sediment loads discharged to the coastal part of the ECS (Jiao et al., 2007), which led to reduced light transparency and reduced phytoplankton production. Thus, the TGD construction reduced sediment inputs from the Changjiang River (Yang et al., 2006), which resulted in increased light availability in the coastal ECS. The effects of the TGD construction on the ecology of Changjiang estuary and in the surrounding ECS have been reported by many researchers (Gong et al., 2006; Jiao et al., 2007; Song et al., 2008; Wang et al., 2011). Furthermore, the number of tropical cyclones increased after 2000 (Lee et al., 2012), which further favoured diatoms because of increased mixing; in the absence of stratification, upwelling promotes the occurrence of diatom blooms in continental shelf areas (Yoder et al., 1983). Humborg et al. (1997) also observed a rapid decline in the Si:N ratio and consequent changes in

phytoplankton composition and cell density in the Black Sea as result of dam construction in the Danube River, and reported that the coccolithophore group became the dominant phytoplankton community.

4.3 Changes in diatom species composition and light conditions

Decadal variations in diatom mean irradiance indicate that phytoplankton light availability has fluctuated in the ECS over the past 50 years. Laboratory experiments showed that the concentrations of protective pigments decreased and the concentrations of light harvesting pigments increased at low irradiance density, and that the concentrations of light harvesting pigments decreased and protective pigments increased at high irradiance density (Van De Poll et al., 2005). Generally, low values of the Plan:Tabn ratio are considered to reflect dominance of benthic diatoms, and are related to mixing processes and improved light conditions in the water column, whereas lower diatom mean irradiance is an indication of decreased irradiance in the water column.

The lower ratios of diatom mean irradiance before period III seem to indicate increased availability of light that would have induced diatom production. However, the high values of the Plan:Tabn ratios in these periods indicate that planktonic diatom species dominated the diatom community, which further implies that benthic diatoms were limited by light. The dominance of benthic diatoms after 2001 clearly indicates increased availability of light. After 2001, the Plan:Tabn ratio decreased noticeably, implying greater production of benthic diatoms than planktonic diatoms. In highly turbid waters the relative abundance of planktonic diatoms increases at the expense of benthic diatoms (Weckström and Juggins, 2005); however, in this study, benthic diatom abundance overwhelmingly increased when the light conditions improved. Phytoplankton production in coastal parts of the ECS, and particularly in areas close to the Changjiang Estuary, frequently experienced light limitations (Zhu et al., 2009), which further suggests that increases in incoming irradiance in the water column may trigger high primary production of benthic diatoms.

Suspended inorganic particles attenuate the light that penetrates into the deep water column and interferes with phytoplankton photosynthesis (Kirk, 1983). Recently, Liu et al. (2013) reported that the cell density and growth rates of *Phaeodactylum*

tricornutum Bohlin and *Gymnodinium* sp. decreased as a result of increased suspended particles. On the other hand, Guenther and Bozelli (2004) showed that phytoplankton density decreased because of light limitations caused by bauxite tailings and inorganic turbidity in Amazonia Lake, Brazil. Furthermore, Yoder (1985) discussed limitations of photosynthesis because of high turbidity in coastal waters across the southeastern continental shelf of the South Atlantic Bight. High primary production was limited to the upper part of water column in the coastal zone of the central Georgia embayment, and high turbidity in this area was the result of suspended particles (Oertel and Dunstan, 1981). Similarly, Randall and Day Jr (1987) reported light-limited primary production across the Louisiana estuary because of high turbidity. Thus, the dominance of benthic or neritic diatoms such as *Paralia salcata*, *Actinoptychus senarius* and *Thalassionema nitzschioides* during the past 10 years is most probably associated with the decreased sediment influxes from the Changjiang River that have resulted from the construction of the TGD (Wang et al., 2011) and consequent increases in light availability.

The increased concentrations of diatom irradiance protective pigments (diatoxanthin+diadinoxanthin) and Chl-*a* between 2001 and 2011 were the result of increased irradiance and a consequent increase in primary production. Regardless of the fact that the D+DD/TChl-*a* ratio should increase when irradiance increases in the water column, as indicated by the Plan:Tabn ratios, the increases in the fucoxanthin and Chl-*a* concentrations from 2001 to 2011 coincided with decreased D+DD/Chl-*a* ratios. This resulted from a very dramatic increase in the TChl-*a* concentration (420%), which in turn was probably related to an increase in the relative abundance of benthic diatoms associated with the increased intensity of the available irradiance. Furthermore, this decrease in diatom irradiance probably resulted from high Chl-*a* production by other algal groups.

5 CONCLUSION

The long-term trends in diatom and dinoflagellate marker signatures indicate that there was variation in the decadal productions of both of these phylogenetic groups. Diatoms dominated in the periods before 1982 and after 2001; inputs of nitrogen fertilizer were low before 1982, while after 2001, the TGD construction impacted on the coastal ECS. Dinoflagellate production increased between 1982

and 2001 and coincided with increased nitrogen fertilizer inputs and a warm-wet phase. However, on the decadal time scale, the production of dinoflagellates has been increasing up to the present. The dramatic change in diatom abundance and most pigment signatures from 2001 to 2007 implies that there have been substantial biogeochemical changes in the coastal area of the ECS as a result of the construction of the TGD. Further studies of dinoflagellate cell counts and species composition in the inner, mid, and outer shelf of the ECS and the NW Pacific Ocean will contribute to an improved understanding of these two major phytoplankton groups and their decadal-scale dynamics.

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