

Changes in upwelling mechanisms drove the evolution of marine organisms

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ABSTRACT

Long-term evolution is thought to take opportunities that arise as a consequence of mass extinction (as argued, for example, by Gould, 2002) and the following biotic recovery, but there is absolutely no evidence for this being the case. However, our study shows that eutrophication by oceanic mixing also played a part in the enhancement of several evolutionary events amongst marine organisms, and these results could indicate that the rates of oceanic biodiversification may be slowed if upwelling becomes weakened by future global warming. This paper defines three distinct evolutionary events of resting spores of the marine diatom genus *Chaetoceros*, to reconstruct past upwelling through the analysis of several DSDP, ODP and land-based successions from the North, South and equatorial Pacific as well as the Atlantic Ocean during the past 40 million years. The Atlantic *Chaetoceros* Explosion (ACE) event occurred across the E/O boundary in the North Atlantic, and is characterized by resting spore diversification that occurred as a consequence of the onset of upwelling following changes in thermohaline circulation through global cooling in the early Oligocene. Pacific *Chaetoceros* Explosion events-1 and -2 (PACE-1 and PACE-2) are characterized by relatively higher occurrences of iron input following the Himalayan uplift and aridification at 8.5 Ma and ca. 2.5 Ma in the North Pacific region. These events not only enhanced the diversification and increased abundance of primary producers, including that of *Chaetoceros*, other diatoms and seaweeds, but also stimulated the evolution of zooplankton and larger predators, such as copepods and marine mammals, which ate these phytoplankton and plants. Current thinking suggests new evolutionary niches open up after a mass extinction, but our study finds that eutrophication can also stimulate evolutionary diversification. Moreover, in the opposite fashion, our results show that as thermohaline circulation abates, global warming progresses and the ocean surface becomes warmer, many marine organisms will be affected by the environmental degradation.

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1. Introduction

Primary producers are diverse and widespread strongly reflecting their environment and are usually the first to respond to environmental forcing, especially changes in nutrient supply, making them excellent paleoceanographic indicators. Diatoms are the dominant group of phytoplankton in the modern oceans, they account for approximately 40% of total oceanic primary productivity and over 50% of organic carbon burial in marine sediments (Tréguer et al., 1995; Falkowski et al., 2004). Coastal upwelling areas represent only 1% of today's oceans, but the primary production in these upwelling areas accounts for 90% of the global primary production (Ryther, 1969; Nelson et al., 1995). Of the diatoms, the marine genus *Chaetoceros* is one of the most important marine taxa contributing to ~20–25% of total marine primary productivity in near-shore upwelling regions, as well as in coastal areas (Rines and Theriot, 2003). As nutrient supplies are depleted through

the course of seasonal upwelling, most species form thick-walled resting spores, which sink to the sea floor where they await the return of favorable conditions (McQuoid and Hobson, 1996). These heavily silicified resting spores are preserved as fossils in sediments, frequently in near-shore sediments in association with other fossil diatom valves. The resting spores represent a significant part of the fossil marine diatom assemblage, providing useful information for reconstructing past productivity and environmental change (Akiba, 1986). Traditionally, diatom-rich sediments have been used to infer the presence of upwelling where nutrient-rich waters are brought to the surface. Thus the abundance of *Chaetoceros* resting spores in sediments and in the water column has also been treated as an indication of diatom productivity, and the presence of upwelling and nutrient fluctuation in shallow coastal environments (Sancetta, 1982; Akiba, 1986). However relatively little attention has been given to fluctuations of *Chaetoceros* resting spores in Earth history because of taxonomic difficulties (Suto, 2003). Yet, over the past decade, this situation has gradually started to improve, largely through a better taxonomic understanding of *Chaetoceros* resting spores (e.g. Suto, 2006b,c, 2007), which has become widely accepted.

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Akiba (1986) showed a high abundance event of *Chaetoceros* resting spores in the late Miocene in northern Pacific regions during a routine count of “usual” diatom valves and mentioned that the high *Chaetoceros* abundance was caused by bottom current winnowing or the influence of neritic or shallow-water environments. On the other hand, Suto (2006a) identified a mass occurrence and evolutionary diversification event of *Chaetoceros* resting spores from Eocene–Oligocene cores in the Norwegian Sea, and indicated that a drastic change in nutrient supply from a stable and seasonal upwelling system in the Eocene to an unstable and sporadic system in the Oligocene accounted for this event. Moreover, he mentioned that *Chaetoceros* flourished from the Oligocene onwards, rose to dominance over dinoflagellates and/or nannoplankton which were the main producers prior to the Eocene. A significant consequence of the importance of *Chaetoceros* in marine primary production is that these *Chaetoceros* events likely affected the food chain in coastal regions and subsequently the evolution of several marine organisms living in these coastal regions and/or open oceans. However, our knowledge of the distribution and abundance patterns of *Chaetoceros* is relatively poorly known and thus the influence of such abundance events on other marine organisms and their evolution is uncertain.

Recently, by correlating data from phytoplankton fossils (e.g. Neptune database of Spencer-Cervato, 1999), the fossil records of several marine mammals (e.g. Fordyce and Barnes, 1994) and oxygen isotope records (expressed as $\delta^{18}\text{O}$ values, a proxy reflecting both temperature and global ice volume; e.g. Zachos et al., 2008) with tectonic and climatic changes (e.g. Whitehead et al., 2008), several authors have promoted revolutionary ideas that the evolution of diatoms must have played an important role in the evolution of other marine organisms. This concept suggests that evolutionary triggers were caused by oceanic environmental and tectonic fluctuations such as ocean mixing pattern and overall cooling of the planet that began after the opening of Drake Passage in the late Eocene (Berger, 2007; Steeman et al., 2009; Marx and Uhen, 2010). These authors also discussed that a changing food supply drives evolution in the sea. However, the diatom information which they used is mainly compiled from raw occurrence data from ocean drilling projects operated from the 1960s to the recent and therefore contains inherent problems because they did not consider the “development” of taxonomic studies and concepts. Moreover, the data includes a lot of synonymies. For example, *Denticulopsis lauta*, an important diatom taxon for Miocene biostratigraphy, was described as one species in Simonsen and Kanaya (1961) and has been since divided into more than 20 taxa (e.g. Yanagisawa

and Akiba, 1998; Watanabe and Yanagisawa, 2005). As a result, the fluctuations in diatom diversity based on old taxonomic and biostratigraphic concepts are suspect and their results are still under discussion. Thus far, there has been little consideration of how diversification of some of these groups was influenced by the availability of food sources (e.g. different diatom taxa). A review, using the most current taxonomic concepts is therefore needed to know the true evolutionary relationship between phytoplankton, marine animals and tectonic history.

In this paper we use the widely accepted taxonomic concepts of *Chaetoceros* resting spores by Suto (2003, 2007) to clarify the stratigraphic changes and evolutionary history of this genus using sediment samples from the Deep Sea Drilling Project (DSDP), Ocean Drilling Program (ODP), Integrated Ocean Drilling Program (IODP) and land sections deposited during the past 40 million years (Fig. 1). Here we show three distinct resting spore events recognized across the Eocene/Oligocene (E/O) boundary (ca. 33.7 Ma), in the late Miocene (ca. 8.5 Ma) and late Pliocene (ca. 2.5 Ma) when marine thermohaline conditions changed dramatically after tectonic and climatic events, and then we discuss how these events provided the evolutionary trigger for several marine organisms such as whales.

2. Materials and biostratigraphy

2.1. Atlantic samples: middle Eocene to middle Miocene

To better understand Eocene–Oligocene palaeoceanographic and palaeoclimatic events in the high and middle northern latitudes in the Atlantic Ocean, silty to muddy samples from five key DSDP/ODP sites (DSDP Leg 38 Site 338 and ODP Leg 151 Holes 908A and 913B in the Norwegian–Greenland Sea, and DSDP Leg 41 Site 366 and Hole 369A in the eastern equatorial Atlantic; Fig. 1), containing well-preserved and abundant diatom and resting spore assemblages, were investigated by calibrating *Chaetoceros* resting spore events to the ‘normal’ (i.e. the diatom assemblage except for *Chaetoceros* resting spores) diatom assemblage. Calcareous nannoplankton and diatom biostratigraphy were mainly used to determine the age of the sediments (Fig. 2).

2.1.1. DSDP Leg 38 Site 338

Sediments from Site 338 (67° 47.11' N, 05° 23.26' E; water depth 1297.0 m) were recovered during DSDP Leg 38, which cored lower

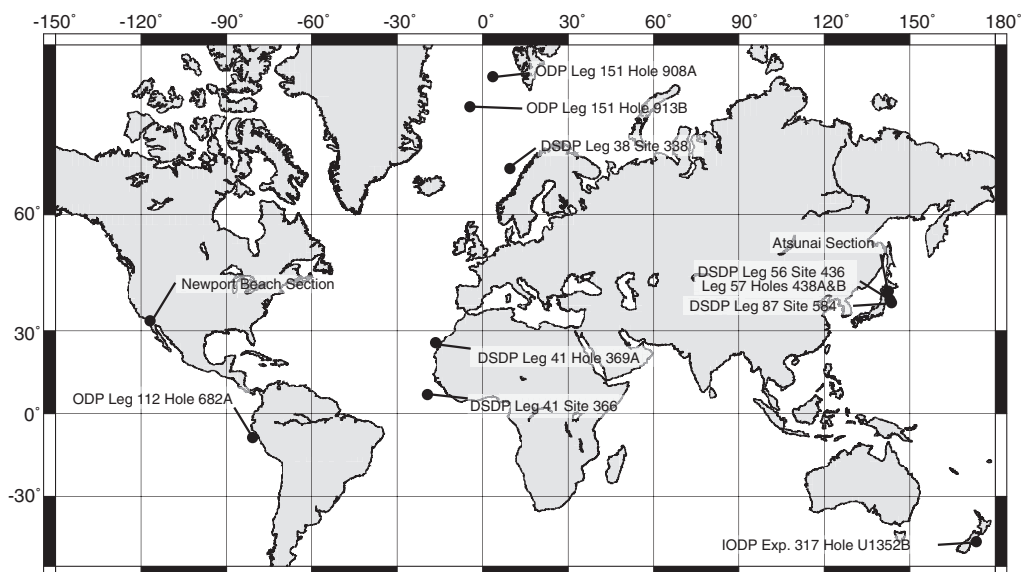


Fig. 1. Map showing sample positions from the Deep Sea Drilling Project (DSDP), the Ocean Drilling Program (ODP), the Integrated Ocean Drilling Program (IODP) Sites and Holes and the Atsunai and Newport Beach Sections.

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