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Intra- and infra-specific morphological variation in selected coccolithophore species in the equatorial and subequatorial Pacific Ocean

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Abstract

The ecological preferences of morphological groups within major coccolithophore taxa were studied in surface water samples from the equatorial and subequatorial Pacific Ocean. *Emiliania huxleyi* was subdivided into three morphological groups: Type A, Type C, and variety *corona*. The most probable factors limiting the occurrence of *E. huxleyi* Types A and C were high temperatures and low nutrient concentrations, respectively. *E. huxleyi* var. *corona* had an affinity for oligotrophic conditions. *Calcidiscus leptoporus* ssp. small was adapted to fertile waters. *Umbilicosphaera foliosa* and *Umbilicosphaera sibogae* preferred mesotrophic upwelling waters and stratified marginal waters surrounding the upwelling front, respectively. Among the three *Umbellosphaera tenuis* morphotypes observed in this study (Types I, III, and IV), only Type I was found in very warm tropical surface. Both Types III and IV were found in subtropical waters, and Type III differed from Type IV in that its distribution was constrained to hemi-pelagic waters. Habitat segregation among the morphotypes of major taxa indicates that the observed global distributions of these major taxa are, in fact, combinations of discrete morphological groups.

Keywords: Coccolithophore; Extant; Morphological variation; Biogeography; *Emiliania huxleyi*; *Calcidiscus leptoporus*; *Umbilicosphaera*; *Umbellosphaera*

1. Introduction

In a typical coccolithophore population, only 1–5 abundant taxa represent over 60% of the assemblage, while the remainder is composed of 10–40 rare taxa, each of which contribute to less than 5% (e.g., Hagino and Okada, 2004; Thierstein et al., 2004). Most studies of living coccolithophores refer to the abundant taxa as major taxa, and focus on their ecology. The composition of the major taxa differs among water masses. Subpolar assemblages are dominated by *Emiliania huxleyi*, and often contain *Coccolithus pelagicus*. The surface assemblages in oligotrophic warm waters consist of abundant *Umbellosphaera irregularis* or *Umbellosphaera tenuis*. In warm eutrophic waters, *Calcidiscus leptoporus*, *E. huxleyi*, or *Gephyrocapsa* spp. comprise the greater part of the flora (e.g., Jordan and Chamberlain, 1997; Hagino and Okada, 2004). Most of these major taxa display intraspecific morphological variation in their coccoliths, and are subdivided into morphological groups (e.g., Young et al., 2003).

Extensive distributions of morphological groups of *Gephyrocapsa* spp. and *C. leptoporus* have been docu-

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mented in the Atlantic Ocean. For example, Bollmann (1997) classified medium-sized *Gephyrocapsa* from marine surface sediments into five morphotypes with discrete environmental preferences. Extant *C. leptoporus* can be subdivided into at least three size groups: large, intermediate, and small forms. The intermediate form is dominant while the large form tends to be more abundant in warm waters (e.g., Knappertsbusch et al., 1997; Ziveri et al., 2004). In the Pacific Ocean, the detailed distribution of morphological subgroups has not been studied, even though the morphotype assignments of selected species have been examined in several studies. McIntyre et al. (1970) showed horizontal distributions of morphotypes of *C. leptoporus* over the entire Pacific. Okada and Honjo (1973b) determined the morphotype assignments of *E. huxleyi* and *C. leptoporus* in the central North Pacific Ocean. Hagino and Okada (2004) separated *E. huxleyi*, *C. leptoporus*, *U. irregularis* and *U. tenuis* into several morphological groups during their original floral observations, but combined the groups at the species level in their floral analysis.

Recent studies have revealed that morphological variation observed in the major species often reflects genetic differences. *E. huxleyi* Types A and B are distinguishable not only by coccolith morphology, but also by immunological responses (Young and Westbroek, 1991; Medlin et al., 1996). Also Schroeder et al. (2005) discovered a genetic marker to separate *E. huxleyi* Type A from Type B. The largest form of *Calcidiscus* (>8 μm) is distinguishable from smaller forms in the life-cycle association with holococcoliths, and by molecular genetics; therefore, it has been raised to species rank as *Calcidiscus quadriperforatus* (Geisen et al., 2002; Sáez et al., 2003). Extant Coccolithus consist of two morphological groups that can be differentiated by size, and ecology, and which produce different holococcoliths during the haploid phase of the life-cycle (e.g., Cachão and Moita, 2000; Geisen et al., 2002). Molecular phylogenetic studies have shown a sufficient number of substitutions in the base sequences of these morphological groups to raise them to species rank, with the large temperate groups as *Coccolithus braarudii* and the small sub-polar groups as *C. pelagicus* (Sáez et al., 2003; Geisen et al., 2004). Sáez et al. (2003) have concluded that *Umbilicosphaera foliosa*, which has often been classified as a variety of *Umbilicosphaera sibogae*, is a discrete species, based on differences in morphology and molecular phylogenetics. These results suggest that the traditional species-level classification is too coarse to recognize true coccolithophore biodiversity, and a more refined taxonomy is required to discuss the ecology of coccolithophores.

Here we present information on the horizontal distributions of morphological groups observed in *E. huxleyi*, *C. leptoporus*, *U. foliosa*, *U. sibogae*, *U. irregularis*, and *U. tenuis* in the equatorial–subequatorial Pacific Ocean by combining the published quantitative data by Okada and Honjo (1973b), and unpublished data obtained during the studies for Hagino and Okada (2004). The aim of this study is to reveal the habitat preferences of the morphological groups for each major species in order to understand true coccolithophore ecology.

2. Oceanographic setting

The equatorial and subequatorial Pacific (20°N–20°S) is characterized by seven major surface currents: westward-flowing North and South Equatorial Currents (NEC and SEC), eastward-flowing North and South Equatorial Counter Currents (NECC and SECC), western boundary flows of the Philippines and East Australian Currents, and the eastern boundary Peru/Chile Current (Fig. 1). The NEC is the south boundary current of the North Pacific subtropical Gyre. The strong westward flows of the NEC and SEC arrive at the Philippines and Indonesian archipel-

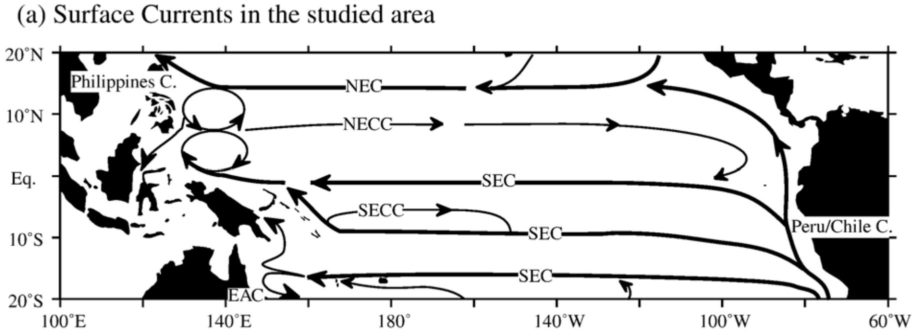

Fig. 1. Distribution of the surface currents in the equatorial and subequatorial Pacific Ocean.