

New approaches and progress in the use of polar marine diatoms in reconstructing sea ice distribution

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Abstract Reconstructing the paleo-latitude extent of sea ice in the Southern Ocean over time can be accomplished using modern diatom data. However, it is more difficult to extend the utility of diatom proxies farther back in time, to time periods characterized by species that are now extinct, since we are uncertain of the paleoenvironmental affiliation of those species we can't observe in modern assemblages. We propose several research strategies to strengthen our ability to use diatom data to reconstruct sea ice history. These tactics include the evaluation of specific morphologic characteristics and distinct taxa, as well as the identification of specific adaptations that may have evolved following the initiation of sea ice in the Southern Ocean.

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Introduction

A major objective of Southern Ocean paleoceanography is to reconstruct the distribution of annual sea ice cover over time. Specifically, researchers are interested in tracing both the initiation of sea ice development, as part of the long term development of the cryosphere, and tracking changes in the spatial and temporal extent of sea ice since its inception. As outlined by Armand and Leventer (2003), interest in sea ice reconstruction is linked to its role in regulating climatic, oceanographic and biological systems. Climatically, these links include the role that sea ice plays in heat and gas exchange in polar oceans (Maykut, 1978) and its high albedo (Eicken, 2003; Haas, 2003). Sea ice formation is critical in the formation of dense bottom waters (Dieckmann and Hellmer, 2003); conversely, sea ice melt results in stabilization of the upper water column (Smith and Nelson, 1986) and these ice edge zones are commonly sites of enhanced levels of primary productivity (Smith and Nelson, 1985; Arrigo and van Dijken, 2003). Sea ice biota are dominated by diatoms (Garrison et al., 1986) and during winter, when phytoplankton are scarce, sea ice diatoms are an important food source for the dominant species of Antarctic krill – *Euphausia superba* (Marschall, 1988; Frazer et al., 2002). Finally, sea ice data are necessary inputs to climate models, especially important considering the potential positive feedback role played by sea ice (Petit and Norro, 2000). For example, modelling work of DeConto et al. (2007) has demonstrated the value of sea ice diatom data for inferring the thermal state of Antarctic glaciation. Their work showed that if the East Antarctic ice sheet (EAIS) is polythermal, warm, and/or dynamic, there will be no sea ice or sea ice flora. If the EAIS is cold polar, then there may be sea ice and sea ice flora. Thus, the sea ice diatoms are the best proxy for the presence of cold ice sheet conditions.

Reconstruction of sea ice distribution has been accomplished via a variety of proxies, including microfossil assemblages, and geochemical and sedimentologic tracers (see review in Armand and Leventer, 2003). Microfossil approaches based on polar marine diatoms in particular, are relatively straightforward, and have been successfully applied over time scales when the species assemblages are represented by extant species with which modern day correlation tools be applied, between these modern species and their environmental preferences. This approach relies upon both the abundance and diversity of diatoms in the polar ocean, with many species associated with either the sea ice and/or the marginal ice zone (Gleitz et al., 1998). These relationships and the ultimate usefulness of Antarctic “sea ice diatoms” as paleoenvironmental indicators have been reviewed by Leventer (1998) and Armand and Leventer (2003); in general, researchers have demonstrated that we can reconstruct recent Southern Ocean sea ice history based on modern diatom data.

In this abstract we discuss the following question: Can diatom data be used reliably to reconstruct sea ice history in time periods characterized by species that are now extinct? The fundamental dilemma is how we can be certain of the paleoenvironmental affiliation of any particular species if we can't observe it in modern assemblages. In addressing this problem, two lines of investigation are explored. First, given a uniformitarian approach to geology and the common assumption that “the present is the key to the past,” it is necessary to determine whether specific morphologic characteristics or diagnostic taxa can be used as indicators of sea ice and/or ice edge environments. Second, since the presence of seasonal ice cover has had a significant impact on all aspects of the polar ecosystem throughout its glacial history, it is possible that specific types of adaptations, such as the development of resting spores or more heavily silicified winter stages, may have evolved following the initial or persistent occurrence of annual sea ice. This possibility needs to be addressed, through a thorough review of the available literature. Application of the approaches described above, indicates the presence of sea ice in the Southern Ocean during the late Miocene (Harwood and Bohaty, 2007).

Discussion

A key question to be addressed is how can we identify potential sea ice indicators among extinct taxa based purely on their morphological features? The first step in addressing this question is to identify those Southern Ocean diatoms that are specifically associated with sea ice. Armand et al. (2005), for example, present a comprehensive review of the biogeography of Southern Ocean sea ice taxa, defining “sea ice related species as those confined southward of the Polar Front generally observed within the Sea Ice Zone (Tréguer and Jacques, 1992) and with a known presence within, on or under sea ice or in the water column surrounding sea ice.” (Armand et al., 2005, p. 95) In particular, they review the documented distribution of a suite of species that are commonly found in Southern Ocean sediments, and describe their affiliation with sea ice. These species include *Actinocyclus actinochilus*, *Fragilariopsis curta*, *Fragilariopsis cylindrus*, *Fragilariopsis obliquecostata*, *Fragilariopsis rhombica*, *Fragilariopsis ritscheri*, *Fragilariopsis separanda*, *Porosira glacialis*, *Porosira pseudodenticulata*, *Stellarima microtrias*, *Thalassiosira tumida* and the *Thalassiosira antarctica* group. One tactic that could be taken is to review the evolutionary lineages of each of these species to see if their modern forms originated around the same time.

In tagging species as diagnostic of sea ice, several kinds of affiliations are possible. First, some species appear to be “obligate” sea ice forms, well-adapted to living within the sea ice but unsuccessful in open water. A second group of sea ice diatoms thrive in the marginal ice zone; these are primarily seeded from melting sea ice. Finally, since sea ice forms as sea surface temperatures drop below the freezing point, some species may not be found thriving within the sea ice, but may have morphologies that are temperature-dependent, with colder and warmer water forms easily distinguished (sometimes referred to as “winter” and “spring” forms, respectively).

A reliable tracer in marine sediments of overlying sea ice is the occurrence of members of the first group of “sea ice diatoms,” that is, those species whose living distribution appears to be limited to within the sea ice. This group includes species such as *Pleurosigma antarcticum*, *Pinnularia quadratarea*, *Nitzschia stellata*, *Entomoneis kjellmanii*, and *Berkeleya adeliensis*. These species are most common in congelation, platelet and strand ice communities (see review in Leventer, 1998). However, despite their abundance in these kinds of sea ice, they are under-represented in the underlying sediments, so their absence in sediment samples can’t be used to rule out the presence of sea ice. Most of these species are thinly silicified, hence dissolution in the water column and at the sea floor is the most likely cause for their under-representation in the sediments (Leventer, 1998). Of the group listed above, only *Pinnularia quadratarea* is relatively heavily silicified, leading Leventer (1998) to suggest that this species is more promising as a sea ice indicator. Its usefulness is limited, however, to coastal areas where congelation ice is common.

Consequently, most studies that reconstruct sea ice distribution rely on the use of those species that are common in the marginal ice zone, such as (but not limited to) *F. curta* and *F. cylindrus*. (e.g. Jordan and Pudsey, 1992; Buffen et al., 2007) These species are common in sea ice, and as the sea ice melts, are seeded successfully into the adjacent open water. Leventer (1998) suggested that the seeding success of these two species, as contrasted to those species exclusively successful in the ice, may be related to their small size, short chain lengths, and consequent low settling rates. Given these observations, we suggest that an initial assessment of the evolutionary lineages of these two species may help our efforts toward understanding the earliest development of sea ice in the Southern Ocean.

Another strategy to pursue is evaluating the relationship between initiation of annual sea ice cover and the occurrence of resting spores and/or more heavily silicified winter stages. Fryxell (1994) discussed three parallel evolutionary strategies that promote winter survival in diatoms. These strategies include the production of resting spores, winter growth stages and cold water stages. All three strategies are noted by valves that are more heavily silicified, an advantage in increasing sinking rates out of surface waters where sea formation is taking place (Fryxell, 1988). In addition heavily silicified cells may suffer less damage during zooplankton grazing (Fryxell, 1988). Fryxell (1994) also noted that given that all of these strategies produce relatively heavily silicified valves, these valves are often better preserved in the sediments than their lightly silicified counterparts.

Resting spores, non-vegetative cells that “must germinate before normal vegetative division” (Fryxell, 1994, p. 438), are observed in genera such as *Chaetoceros*, *Porosira*, *Thalassiosira*, *Odontella* and *Stellarima*, but in general, are not that common in Antarctic species (Fryxell, 1994). Fryxell (1994) suggests that winter growth stages, as illustrated by *Eucampia antarctica*, and cold water stages, as observed in *Thalassiosira tumida*, for example, present alternative strategies to resting spores, that have the advantage of permitting continued growth under the less optimal environmental conditions generally experienced during the winter. Winter growth stages, as contrasted to resting spores, are not packed with lipids, but rather remain vacuolate; these cells can continue to reproduce during the winter as light levels permit (Fryxell, 1994). Winter cells of *Proboscia truncata* have also been shown to reproduce (Jordan et al., 1991). The most thorough experimental work on cold water stages was completed by Fryxell (1988), who studied two clones of *T. tumida*, cultured under a range of temperature and salinity conditions. While salinity had no obvious effect on valve morphology, cells cultured at lower temperatures were more heavily silicified and less well fasciculated. Field observations produced similar results, with specimens found in areas of sea ice formation marked by their heavy silicification and linear array of areolae (as opposed to fasciculated) (Hasle et al., 1971). Fryxell (1994) noted that polymorphism is a common trait of Antarctic diatoms and suggested that it may be a response to seasonal temperature change. Other species that exhibit polymorphism, that might be useful in terms of addressing questions concerning paleotemperatures and the presence or absence of

sea ice include *Thalassiosira ritscheri* and *Thalassiosira gracilis* (Fryxell, 1994). Similar to *T. tumida*, *T. ritscheri* has a spring form that is lightly silicified versus a heavily silicified winter form; this change in silicification is associated with a change in fasciculation. *Thalassiosira gracilis* exhibits decreased size with a decrease in silicification. The adaptation of *Rhizosolenia sima* to growth or survival in sea ice is the formation of heavily silicified cells, which can be regarded as a winter form.

Eucampia antarctica, another common Southern Ocean species, has shown promise as a tool to record changes in sea surface temperatures and sea ice. Works by Fryxell (1989) and Fryxell and Prasad (1990) document a northern and southern variety distinguished based on two features. The more northerly (sub-polar) form, *Eucampia antarctica* var. *antarctica*, is characterized by its asymmetry in broad girdle view, while the southern, or polar, variety, *Eucampia antarctica* var. *recta*, is symmetrical in broad girdle view. This variety has been observed, for example, in the autumn near ice in the Weddell Sea (Fryxell, 1989). In addition to its diagnostic asymmetry, chains of cells of the northern variety are more likely to be longer than chains of the southerly variety of *Eucampia antarctica*. Fryxell and Prasad (1990) suggest that under higher light conditions (thinner and/or less sea ice cover) more cell divisions can occur, leading to longer chains. Today, these environmental conditions are typical of more northerly waters of the Southern Ocean. In sediment samples, chain length can be estimated by comparing the number of intercalary versus terminal valves that occur in a sample. Only the free end of a chain, or the terminal valve, can have a pointed morphology; while valves in the interior of a chain are flat ended, permitting valves to attach to adjacent valves. Chains of *Eucampia* growing in the lower light conditions that are expected in colder waters with more sea ice cover are more likely to be short with a consequent higher relative proportion of terminal valves. Fryxell (1989) and Fryxell and Prasad (1990), for example, observed that the symmetric variety of this species occurred more often as short chains and doublets. On the basis of the findings of Fryxell and Prasad (1990), Kaczmarek et al. (1993) introduced a new paleoenvironmental proxy, the *Eucampia* index (ratio of terminal to intercalary valves), to record oscillations of winter sea ice through the late Pleistocene on the Kerguelen Plateau. This same relationship was used by Leventer et al. (2002) to document early Holocene warmth in the western Antarctica Peninsula region. Whitehead et al. (2005) documented low sea ice concentrations during the Pliocene at two ODP sites along the East Antarctic margin and calibrated the *Eucampia* index by comparison of data from surface sediment samples to modern sea ice data. The utility of this index could be improved with more data from the living assemblage.

Detailed ecologic and distributional studies, conducted throughout several seasons, coupled to laboratory culture work can be used to evaluate the controls on polymorphism in diatom species. These morphological adaptations may enable species to survive unfavorable winter conditions within the sea ice, and give them an advantage in early summer of phytoplankton growth. The presence of such forms in sediments may indicate the paleo-latitude range of the sea ice margin.

Summary

Reconstructing the paleo-latitude extent of sea ice in the Southern Ocean over time can be accomplished using modern diatom data. However, it is more difficult to extend the utility of diatom proxies farther back in time, to time periods characterized by species that are now extinct, since we are uncertain of the paleoenvironmental affiliation of those species we can't observe in modern assemblages. We propose several research strategies to strengthen our ability to use diatom data to reconstruct sea ice history. These tactics include the evaluation of specific morphologic characteristics and distinct taxa, as well as the identification of specific adaptations that may have evolved following the initiation of sea ice in the Southern Ocean. In particular, we note that the evolution of resting spores and winter growth forms should be studied more thoroughly.

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