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Surf zone diatoms: A review of the drivers, patterns and role in sandy beaches food chains

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ABSTRACT

The accumulation of high biomass of diatoms in the surf zone is a characteristic feature of some sandy beaches where the wave energy is sufficiently high. A few species of diatoms, called surf diatoms, thrive in this harsh environment. The main processes driving the spatial and temporal distribution of surf diatoms as well as their standing biomass and growth were described twenty to thirty years ago based on studies conducted on the western coast of the United States of America and South African beaches. Since then, over fifty locations around the world have been reported to have surf diatom accumulations with most (three-quarters) of these being in the southern hemisphere. Their occurrence is controlled by physical and chemical factors, including wave energy, beach slope and length, water circulation patterns in the surf zone and the availability of nutrients to sustain the high biomass. The main forces driving the patterns of temporal variability of surf diatom accumulations are meteorological. In the short term (hours), the action of wind stress and wave energy controls the diatom accumulation. In the intermediate time scale (weeks to months), seasonal onshore winds of sufficient strength, as well as storm events are important. Furthermore, anthropogenic disturbances that influence the beach ecosystem as well as large-scale events, such as the El Niño Southern Oscillation, may lead to significant changes in surf diatom populations in the long term (inter-annual). Surf diatoms form the base of a short and very productive food chain in the inshore of the sandy beaches where they occur. However, the role of surf diatoms in the microbial food web is not clear and deserves further studies.

1. Introduction

The surf zones of several exposed sandy beaches present obvious brownish to greenish water discoloration due to the high abundance of diatoms. The cellular growth of flagellates including dinoflagellates is hampered by the turbulence found in surf zones, whereas diatoms are dependent on high turbulence to optimize their nutrient uptake and light utilization. In addition, some diatoms depend on vertical transport to suspend cells or resting spores from the sediment into the water column after sedimentation during calm periods (Reynolds, 2006).

Among diatoms, a few phylogenetically unrelated species, called surf diatoms, are able to successfully exploit the high wave energy conditions at some sandy beaches. A common feature of surf diatoms is their ability to accumulate in the foam by adhering to air bubbles and, by so doing, form brown patches in the surf zone (Lewin and Schaefer, 1983; Talbot and Bate, 1988a). There are seven confirmed surf diatom species: the centrics *Anaulus australis* Drebes *et* Schulz (Anaulaceae), *Attheya armata* (West) Crawford (Attheyaceae), *Aulacodiscus kittonii* Arnott ex Ralfs (Aulacodiscaceae), and the pennates (Fragilariaceae) *Asterionellopsis glacialis* (Castracane) Round and *Asterionellopsis socialis* (Lewin and Norris) Crawford and Gardner (Plate 1). *Aulacodiscus africanus* Cottam, the first described surf diatom, has not been studied since that early record (Van Heurck, 1896). Two other species of *Aulacodiscus*, *Aulacodiscus johnsonii* Arnott in Pritchard and *Aulacodiscus petersii* Ehrenberg are regularly subdominants with other surf diatoms in South Africa (Campbell, 1996) and New Zealand (Campbell, pers. comm.). It appears that surf diatoms thrive exclusively in surf zones, except for *Asterionellopsis glacialis*, which is also a common component of coastal phytoplankton worldwide (Campbell, 1996).

2. Early studies

Surf diatom accumulations are a natural phenomenon known for a long time. During a botanic expedition near the Congo River

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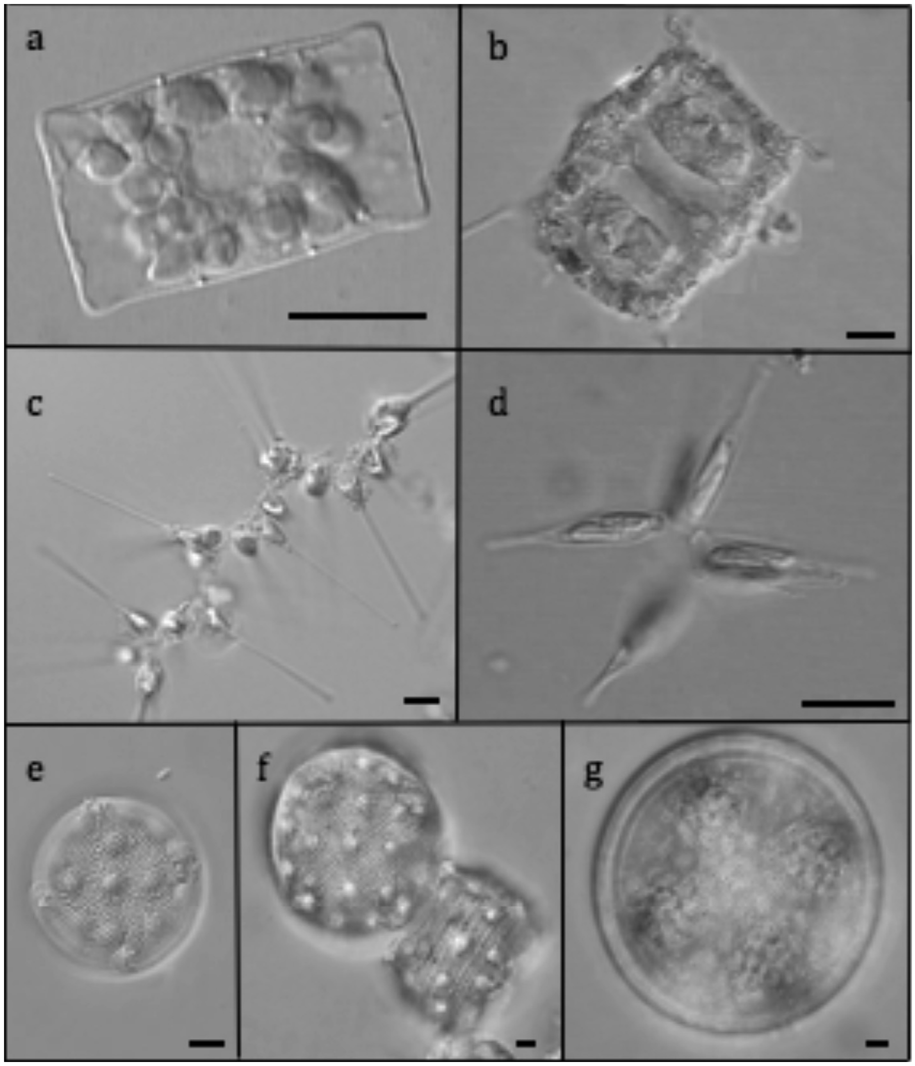

Plate 1. Surf diatoms: a) *Anaulus australis* Drebes *et* Schulz; b) *Attheya armata* (West) Crawford; c) *Asterionellopsis glacialis* (Castracane) Round; d) *Asterionellopsis socialis* (Lewin *et* Norris) Round; e) *Aulacodiscus johnsonii* Arnott; f) *Aulacodiscus kittonii* Arnott; g) *Aulacodiscus petersii* Ehrenberg. Bar indicates 10 μm. No photographs of *Aulacodiscus africanus* Cottam were available.

mouth (West Africa), greenish waters were observed to be due to a high abundance of *Aulacodiscus africanus* Cottam (Van Heurck, 1896). Surf diatom accumulations were first recognized as an important food source in the surf zone of sandy beaches along the Washington coast, western USA (McMillin, 1924). McMillin (1924) identified two species of diatom: a club-shaped small cell associated with wine-red water and another large, round species associated with greenish water. The diatoms were later identified as *Aulacodiscus kittonii*, the species causing greenish waters, and the club-shaped responsible for the "red surf" as *Synedra nitzschioides* Grunow, later described as *Asterionellopsis socialis* (Lewin and Norris) Crawford and Gardner (Lewin and Norris, 1970). At that time, controversial ideas prevailed about the origin of oil and Tolman (1927) postulated its biogenic origin, based on the accumulation of diatoms at Copalis Beach on the Washington coast. This phenomenon at Copalis Beach, was studied in more detail by the American Petroleum Institute, including a preliminary chemical characterization of the "oil" secreted by diatoms (Becking et al., 1927). These authors also came to a general understanding of the diatom accumulations, referring to them as "epidemics", and describing the conditions favoring their occurrence as being towards the end of the rainy season; after a heavy rainstorm; when rains are followed by gentle westerly winds; and when the rain is followed by clear weather and bright sunshine. In the seventies and eighties, studies led by Joyce Lewin revealed the main distribution patterns, species composition, metabolic and ecological processes of Copalis Beach, stressing the importance of surf diatoms as food sources (see review Lewin et al., 1989).

The importance of surf diatoms as main food source of clams was first recognized in New Zealand at the North Island beaches (Rapson, 1954). During the winter, diatom biomass reaching 1.5 kg dry mass m^{-3} was found to comprise mostly *Chaetoceros armatus* Westendorp, now *Attheya armata* (West.) Crawford. *Asterionellospsis glacialis* (Castracane) Round was also present in large quantities at times. It was suggested that the plankton cycle was mainly influenced by the wind regime and in particular to the onshore west winds that coincided with the characteristic phytoplankton flora, in which zooplankton generally "did not thrive" (Rapson, 1954). When the winds switched to easterly, this cycle changed and zooplankton dominated the inshore. The primary production by surf diatoms at Waitarere Beach, New Zealand North Island, reached a maximum of 400 mg C m^3 h^{-1}, but this was probably underestimated by at least an order of magnitude, according to Cassie and Cassie (1960). This production was shown to