

Short Communication

Anthropogenically driven habitat formation by a tube dwelling diatom on the Northern Patagonian Atlantic coast



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ABSTRACT

The tube dwelling diatom *Berkeleya rutilans* (Trentepohl) Grunow plays a key role as early colonizer and bloom former in coastal zones. Exuding large quantities of extracellular polymeric substances (EPS), it can form dense colonies in mucilaginous macroscopic branches, containing thousands of cells. Due to their pronounced three dimensional growths of its mucilaginous structures, it supports a variety of organisms and traps grains and detritus, which makes it an important habitat former and ecosystem engineer, contributing to sediment stabilization, which is a crucial issue in sedimentary areas. In the present study we investigated the identity and structural morphology of *B. rutilans*, blooming in a tidal channel in Northern Patagonia (S40° 43' W64° 56') and experimentally tested its potential physiological responses (e.g. growth rate) to nutrient elevation. The observed morphological plasticity and measured high growth rates under nutrient exposure make *B. rutilans* a likely indicator for eutrophication in sedimentary marine habitats. As to our knowledge the present study provides the first record of *B. rutilans* for Argentinean waters, we discussed the potential reasons for its occurrence and evaluated the ecological impacts of its presence. Due to the observed high colonization capability and rapid response to environmental alterations (e.g. eutrophication, substrate changes) it seems to benefit from human activities, which will consequently favor its further expansion within the disturbed area.

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1. Introduction

Forming dense colonies in mucilaginous macroscopic branches, containing thousands of cells, tube dwelling is a common growth form of diatoms in shallow coastal waters (Lobban, 1983; Sommer, 1997). Due to superficial resemblance to filamentous algae of the brown algal order Ectocarpales (Lewin, 1958; Fricke et al., 2008), tube dwelling diatoms (TDDs) were some of the first diatoms noted by naturalists (Round et al., 1990). By exuding large quantities of extracellular polymeric substances (EPS), TDDs form a mucilaginous matrix surrounding the cells and contribute to the biofilm and finally tube formation (Decho, 1990; Hoagland et al., 1993).

Abbreviations: CLSM, confocal laser scanning microscopy; EPS, extracellular polymeric substances; LM, light microscopy; SAO, San Antonio Oeste; TDDs, tube dwelling diatoms.

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Movement of the cells is thought to be essential for the tube construction (Haupt, 1987) and cells can be often observed gliding within the tubes (Lobban, 1989). Different pennate genera can form tubes, including *Berkeleya* (Cox, 1975), *Cymbella* (Round et al., 1990), *Gyrosigma* (Round et al., 1990), *Navicula* (Cox, 1988), *Parlibellus* (Camacho and Vidal, 2011), *Mastogloia* (John, 1993), and *Nitzschia* (Fernandes et al., 2002). Diatom tubes show variations in chemistry and morphology, and tubes were long-time used next to frustule characteristics to classify TDDs (Grunow, 1880). Thus the tubes of *Berkeleya rutilans* consist mainly of xylans and mannans (Lewin, 1958), while Cox (1981) speculated that the outer tubes of some species may be partially silicified, since they sometimes survive acid cleaning. The role and advantage of diatom tubes is still unclear. It might serve as grazing protection, by lowering the organic content per volume and hinder digestion, whereas the erect growth form may increase the probability of mechanical removal, as discussed by Sommer (1997). As early settlers they can alter the microstructure of early benthic assemblages, and consequently play a crucial role for the further benthic succession (Davis, 2009; Fricke et al., 2015). Overall their macroscopic growth form makes

TDDs unique, important ecosystem engineers in sedimentary habitats. Trapping and binding grains and detritus in their mucilaginous network, they can strongly contribute to sediment stabilization by altering the laminar flow of sediments, changing bottom structure and chemistry, and consequently shape the entire ecosystem (Neumann et al., 1970; Holland et al., 1974). Sensitive to different environmental parameters, TDDs can show seasonal alterations in abundances in shallow coastal waters (Mizuno 1989). The tube like growth form improves nutrient uptake (Sommer, 1997) and diatom development under eutrophic conditions (Hillebrand and Sommer, 1997). Under these conditions, the tube forming *Berkeleya rutilans* strongly increased under nitrogen (N) and phosphorus (P) enrichment. A nutrient polluted intertidal system at the northern Patagonian Atlantic coast, TDDs were observed, forming dense spring blooms (Fricke pers. obs.). Despite their observed high abundances in our research area and their known ecological importance at other sedimentary habitats (e.g. Lobban, 1989; Hillebrand and Sommer, 2000), so far hardly anything is known on the role of tube dwelling diatoms in Argentinean waters. TDDs were identified as important drivers of the benthic succession at an early stage (Fricke et al., 2015). The present study investigated the identity of the dominant early diatom colonizer to learn more about the ecological role of this nutrient driven habitat former. A combined approach of traditional light microscopy (LM) and modern Confocal Laser Scanning Microscopy (CLSM) was used to study the structure of the TDD colonies and to investigate their relation to their associated biota and environment. A morphological and ecological description of the species is presented, which to our knowledge is the first record for Argentinean coastal waters.

2. Material and methods

2.1. Study area

San Antonio Bay (northern Patagonia, Argentina, S40° 43' W64° 56', Fig. 1a,b) is a macrotidal system (up to 9 m) of 80 km² (Aliotta et al., 2000), which shows contrasting trophic conditions within two inner tidal channels (SAO and CONTROL channel) (Martinetto et al., 2010; Teichberg et al., 2010). Providing comparable environmental conditions exposed to similar variations in temperature and salinity, this bivalent channel system offers a unique opportunity to examine the effect of anthropogenic N inputs on receiving waters by comparing the biogeochemical characteristics as done in different studies (Martinetto et al., 2010, 2011; Fricke et al., 2015). Further information on the vegetation and benthic composition can be found in Martinetto et al. (2010) and Fricke et al. (2015), who reported a high abundance of bloom forming green algal genera in the eutrophic SAO channel.

2.2. Nutrient regime

To investigate differences in nutrient concentrations between the two channels during the study period, samples were taken for nutrient analyses at three days (October 21 and 27, November 1 2012). At each sampling day three replicates were collected from each channel at ~10 cm below low tide level, using a sterile (60 ml) syringe, extended with a plastic tube (1.5 m long). Water samples were filtrated (Whatmann GF/F) right after taken and kept cooled (below 4 °C) in 50 ml PE bottles for later standard colorimetric measurements (Kattner, 1999). Concentrations for phosphate, nitrite and silicate were measured for all three days. In addition concentrations for nitrate were determined for the SAO channel at the last two and for the CONTROL channel at the last day.

2.3. Sampling and preservation of field material

A benthic microalgal bloom was observed during October 2012 (spring season, Fig. 1c, d). Tubes of bloom forming algae were randomly sampled from different hard substrates (e.g. stones, rubber of old tires) present in the channel (at approximately 30–50 cm water depth). To study benthic colonization processes, a succession study was initiated, using settlement substrates (PolyEthylene Terephthalate = PET, 1.5 × 2 cm) that were exposed in the eutrophic (SAO) and pristine (CONTROL) channels at 40 cm water depth (below low tide) at sites showing comparable hydrodynamic environments (Fricke et al., 2015). Substrates were sampled (n = 4) after 4 (October 25, 2012), 8 (October 29, 2012), 11 (November 1, 2012) and 40 days (November 29, 2012). More details on sampling procedures can be found in Fricke et al. (2015).

2.4. Mounting and staining

In the laboratory, the substrates and algal material were mounted in semi-permanent slides (SLIDES) using a corn syrup (Karo™ light) solution, diluted with distilled water (1:1) and few drops of 4% formaldehyde to avoid bacterial and fungal growth. Material selected to CLSM analyses was remounted and stained with Congo Red following the protocol of Fricke et al. (2017).

2.5. Microscopical investigation of field material

To investigate the abundances, structure and identity of TDDs and other related benthic taxa, SLIDES were investigated in a three-step microscopic approach: i) *TDD growth rates*, each SLIDE was investigated under LM. To avoid underestimation of patchy distributed colony forming taxa 4 day old assemblages were scanned twice for 15 visual fields (VFs) at 40× (2.55 mm²) and for 10 VFs at 20× (6.8 mm²), whereas 8 and 11 days old assemblages were scanned for 15 VFs at 20× (5.1 mm²) and 40 days old for 15 VFs at 11.5X (0.36 mm²). To investigate the percentage contribution of TDDs to the developing assemblages, measured TDD cover (T) was related to the total taxa cover, calculated as sum from the individual taxa cover (C) as: $T*100/C$. For the following studies, the material was split into two parts. For ii) *TDD colony structures*, one part of the samples (partly stained, see above) were investigated at 20 times magnification, by LM (0.7 numerical aperture; Nikon Eclipse 80i) and CLSM, using a Leica TCS SP5 equipped with a DM5000B upright microscope (Leica, Wetzlar, Germany) and 2 visible light lasers: DPSS 10 mW 561 nm (at 68% power) and HeNe 10 mW 633 nm (at 45% power), combined with the software LAS AF 2.2.1. Leica Application Suite Advanced Fluorescence. CLSM was set following the protocol of Fricke et al. (2017), with excitation range of 620–680 nm and 540–560 nm, emission range of 575–609 nm (ch1) and 665–712 nm (ch 2), gain and offset of ch 1:667 and ch 2:487, pinhole aperture of 59.9 μm, and the amount of light that reached the detectors of ch1:-4.2 and ch2:-0.9. The CLSM data were presented as maximum intensity projections, a sharply focused image using the brightest value along the z-axis for each pixel. Finally for iii) *Species identity*, based on valve characteristics, the other part of the material was removed from the object slides, transferred to a glass vial and prepared according the protocol of Al-Handal et al. (2016). Each sample was mounted on a stub, sputter coated with gold-palladium (SCD 050 Bal-Tec), and investigated using a Tescan VEGA3 microscope (Elekrone-Optik-Service GmbH, Dortmund, Germany) at 15 kV with an SE detector.

3. Results

We observed a pronounced microbenthic spring bloom at the beginning of our study in October 2012 within the highly eutrophic

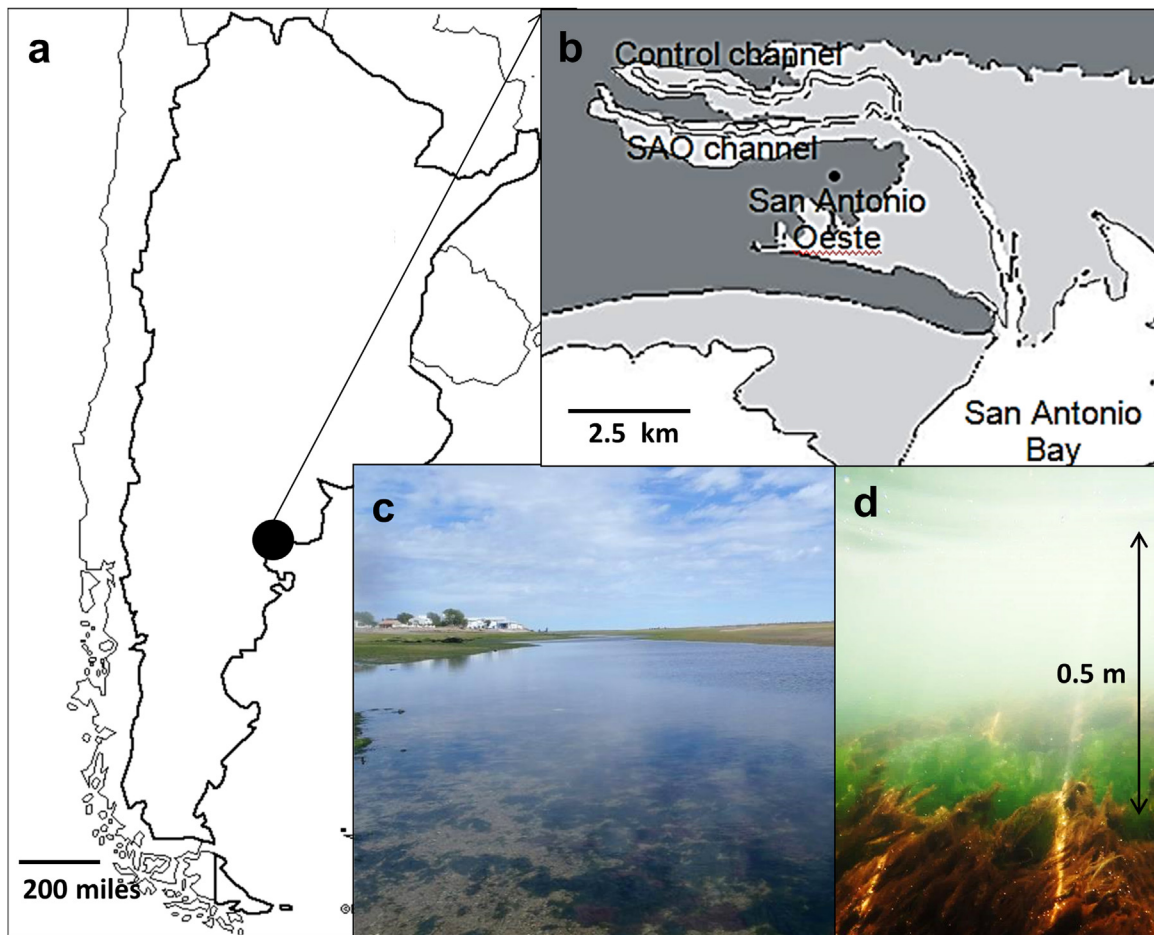


Fig. 1. Overview of study site at San Antonio Oeste (northern Patagonia, Argentina, S40°43', W64°56') (a) and positions of Control and SAO channel, showing the subtidal areas in white and the intertidal zone in grey. (b). Overview of the eutrophied SAO channel in close connection to the town of San Antonio Oeste (c), with bloom of long unbranched tubes of the diatom *Berkleya rutilans*, covering an old car tire at 0.5 m water depth (d).

SAO channel (Fig. 1c). Colonies of *B. rutilans* dominated the diatom community (composed of different species listed in Fricke et al., 2015). Long, unbranched tubes of *B. rutilans* reaching lengths of over 20 cm, were found growing attached to different types of hard substrates. Highest colony densities were observed on stone boulders and old car tires, trashed in the eutrophic channel (Fig. 1d). Comparing the nutrient concentrations of both channels, up to 48 and 103 times higher nitrite and nitrate respectively were found in the polluted SAO channel, whereas comparable values of phosphate and silicate were measured during the bloom (Fig. 2a).

Following the early succession within the polluted SAO and neighbored pristine CONTROL channel, we observed a rapid colonization and increase of tube dwelling diatoms. Already after 3 days we recorded *B. rutilans* on the settlement substrates in both channels, forming about 10% of the benthic assemblages after eight days (Fig. 2b). Interestingly, while *B. rutilans* decreased in the CONTROL channel after 11 days, it strongly increased in the SAO channel, reaching an average of $33 \pm 21\%$ of the benthic assemblage after 40 days.

Diatom colonies were perfectly conserved, which allowed a close investigation of growth forms and thus of the microstructure of the whole microphytobenthic community in LM and CLSM (Fig. 3). Colonies of *B. rutilans* showed strong morphological variations during the study period, potentially related to bloom activity. During high bloom conditions colonies appeared mat-like, composed by long, mainly unbranched tubes (Fig. 3a), reaching several centimeters in length. During the bloom period more and more

branched tubes appeared (Fig. 3b). At the end of the bloom season we observed more compressed, branched, Phaeophycean-like forms (Fig. 3c), composed of multiple layered, inner and outer tubes (Fig. 3d). Overall, *Berkleya* tubes were heavily epiphytized by a variety of organisms, including other diatom species and macroalgal germlings. In addition also endotubular species like *Nitzschia* spp. were observed. CLSM provided a useful tool to distinguish between the densely packed diatom tubes and the associated flora and to unravel the structural interactions.

Cells of *B. rutilans* are linear-lanceolate with rounded ends, wide and rectangular in girdle view, with an apical axis of 26–43 μm and a transapical axis of 7–9 μm . They contain two parietal chloroplasts, connected by a conspicuous central plasmatic connection (H-shaped) (Fig. 3e). SEM showed clear frustule structures with fine striae (32–34 in 10 μm) and irregular pores, frequently elongated near the (not thickened) central area. Raphe endings are slightly curved, with inner endings more than 1/3 frustule length apart (Fig. 3f). Overall the observed specimens were morphologically concurrent to the description of Cox (1975).

4. Discussion

The tube dwelling diatom *Berkleya rutilans* is widely distributed, with records for polar (Scott and Thomas, 2005), temperate (Greville, 1827; Caraus, 2012), and tropical regions (Lobban and Tsuda, 2003). To date the genus comprises over 15 species (algaebase 8.3.15). But this might be an underestimation

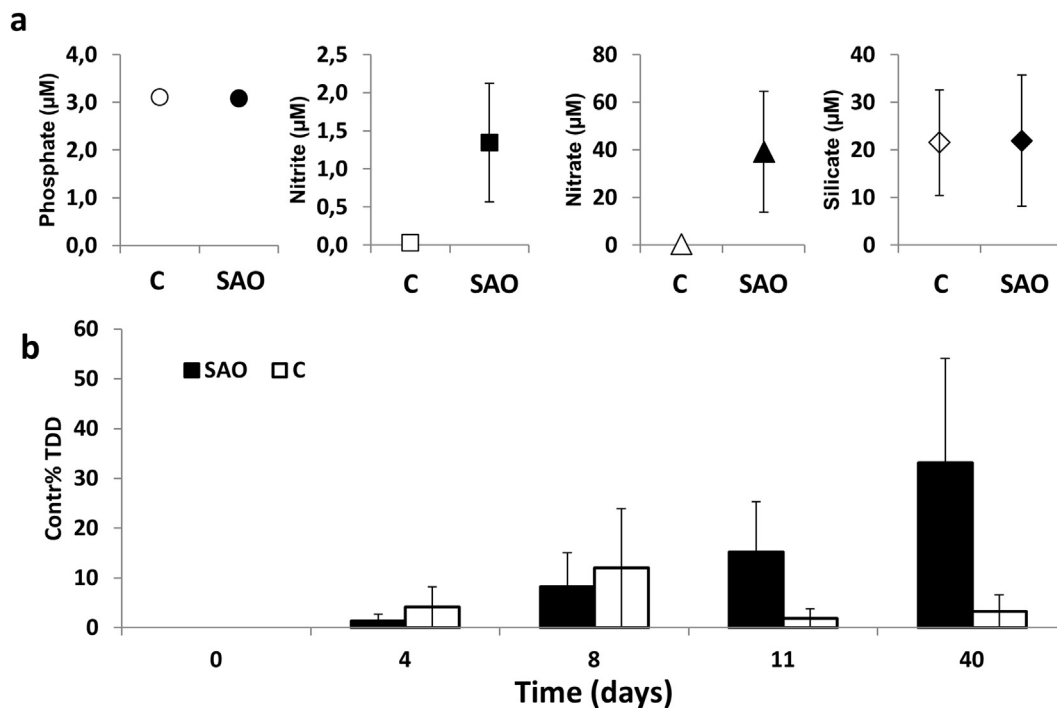


Fig. 2. Nutrient concentrations (a) of Control (white) and SAO channel (black) and Colonization rate of *Berkleya rutilans* (b) growing on artificial substrates (PolyEthylene Terephthalate, 1.5 × 2 cm), exposed in SAO channel (black) and CONTROL channel (white), at 40 cm water depth (below low tide). Graph shows contribution of *B. rutilans* as percentage to total community contribution (contr%). Data shows averages (n = 4) ± SE.

as recent molecular studies on *B. rutilans* (Hamsher and Saunders, 2014) revealed a potential higher diversity.

Proliferation in TDDs is a common phenomenon and reported from different sites, nevertheless the development of high abundances in sedimentary areas is hardly reported (Lobban, 1989; Mizuno, 1989). At our research area, the observable formation of dense spring blooms of *B. r. utilans* might therefore underline a potential ecological importance of this diatom, which seemed to be favored by human driven environmental change. The eutrophic environment of the SAO channel favors the resilience of the developing diatom bloom, as also reported from other sedimentary areas (Hillebrand and Sommer, 1997).

The nutrient driven pronounced macroscopic appearance (bloom) of the otherwise microscopic *B. rutilans* seem to indicate a possible and significant relationship, which could make *B. rutilans* a suitable indicator for eutrophication. In contrast to other drifting planktonic species, its benthic life mode allows this species to accumulate its colonies close to the nutrient source, which might help to detect local nutrient sources (e.g. sewage pipes). Furthermore, in comparison to other known benthic macroalgal indicators (e.g. the green algae *Ulva* spp.), *B. rutilans* provides an important advantage: the structural flexibility of its tubes, allows it to attach and grow on different substrata, which can ease its spread and distribution in sedimentary environments. As known from other studies and areas, artificial structures can strongly alter the benthic communities and their environment (Bers and Wahl, 2004; Geraldi et al., 2013) and also in our study the observed *B. rutilans* bloom, seems to be supported by artificial structures introduced in the area (e.g. car wires). The increasing human activities in our research area might therefore provoke an expansion of *B. rutilans* blooms two-fold, by supporting nutrition and settlement. This consequently will have a strong impact on the adjacent coastal ecosystem. The diatom tubes not only easily overgrow different kinds of substrates, but also contribute to sediment stabilization (Neumann et al., 1970) and support a variety of different algal and invertebrate taxa (Cox, 1975; Lobban, 1989; Sommer, 1997). This is a crucial

point, considering the lack of suitable settlement substrates in the otherwise sandy area. In fact, as observed in the present study the macroalgae-like colonies form three-dimensional microhabitats, supporting different epi- as well as endophytic biota. Considering the temporally bloom formation and the observed changes in tube morphologies over time (from long tubular to branched, multi-tubular tubes), colonies of *B. rutilans* form a rather dynamic habitat with changing properties and a suitable nutrient pool for bacterial decomposition at the end of the bloom season (Lobban, 1989). As only few studies investigated the direct interaction between diatoms and bacteria (e.g. Amin et al., 2012; Senhorinho et al., 2015), it remains unclear how far the growing and also the senescent colonies affect the native bacterial communities. In general, bacterial detoxification driven by senescent benthic blooms can have detrimental consequences for the aquatic ecosystem in still waters (Anderson et al., 2002). In contrast, in turbulent systems, like our study site, “flushed” twice a day due to the immense tidal differences, these harmful effects might be counter balanced, resulting in the observed invertebrate-rich environment (Martinetto et al., 2010). In fact, due to their easy-to-consume erect growth form (Hillebrand and Sommer, 2000), *B. rutilans* might provide an important food source in the research site, as it is commonly grazed by different invertebrates; including isopods (Sommer, 1997) and snails (Lobban, 1989).

Interestingly, despite the observable pronounced spring blooms, and extensive diatom investigations done in the area (e.g. Sar et al., 2001; Sunesen et al., 2008, 2015), there is to our knowledge no record for tube dwelling *Berkleya* in Argentinean waters. This might be explainable by its exclusively benthic life stage and the fact that most diatom studies focused on planktonic assemblages. In addition, its Phaeophycean-like appearance and observed tube plasticity might have led to misleading interpretations and identifications in the past (Lewin, 1958). Another possible explanation might be that the fouling species *B. rutilans* has been introduced to the area, potentially favored by the close proximity to the international trade port San Antonio Este. But, given to the very wide

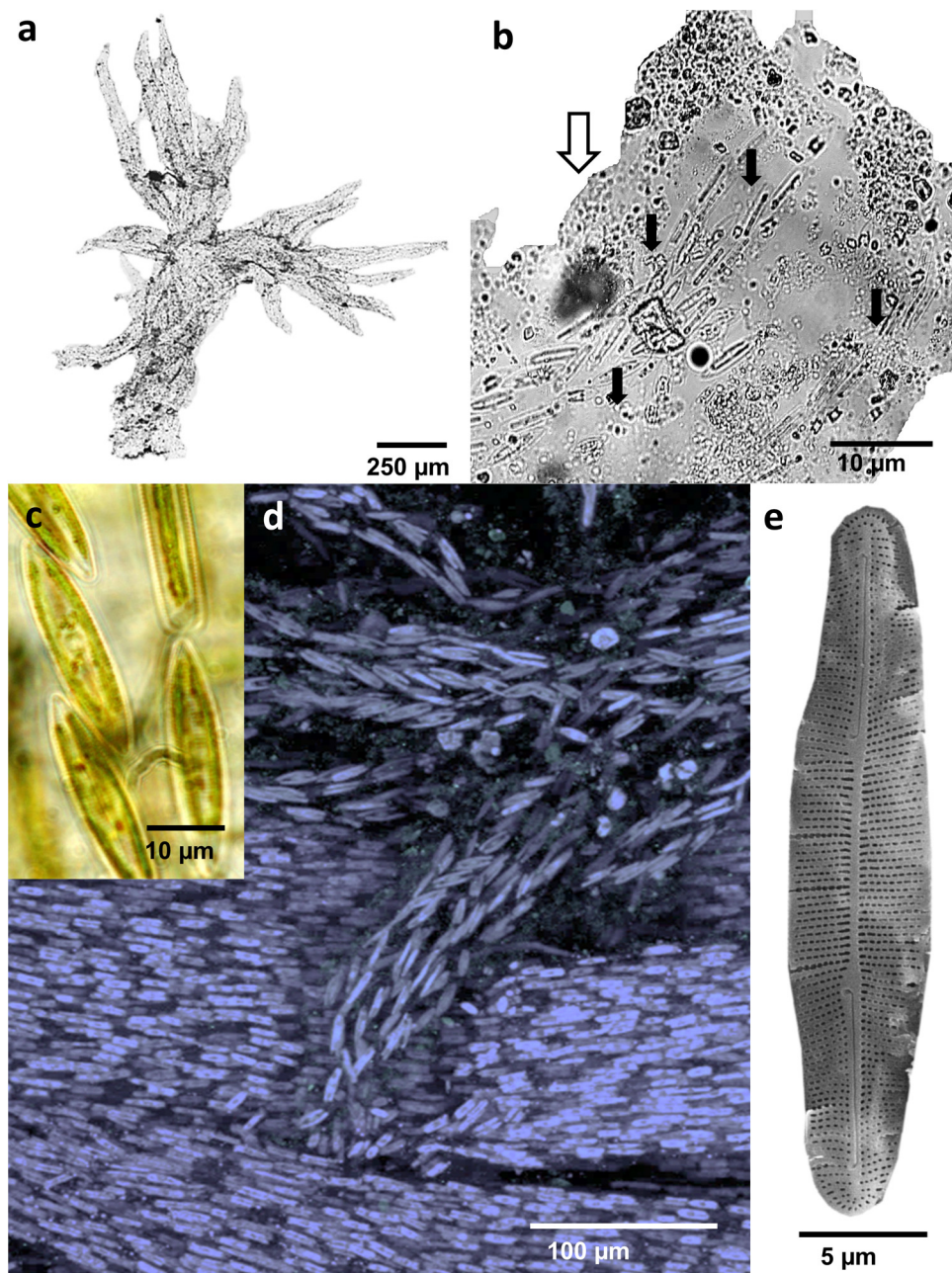


Fig. 3. *Berkleya rutilans* investigated under light microscopy (LM), confocal laser scanning microscopy (CLSM) and scanning electron microscopy (SEM). Pictures showing branched Phaeophycean-like growth form (a), composed of multiple inner (black arrows) and rigid outer tubes (white arrow) (b), inhabited by lanceolate valves showing H-shaped chloroplasts (c) as observed under LM; (d) showing structure of branched and unbranched colonies investigated by CLSM; and (e) showing structure of H₂O₂ cleaned frustule using SEM.

distribution of *B. rutilans* and hidden diversity within the species complex (Hamsher and Saunders, 2014), a recent introduction does not seem to be very likely. It might be therefore more probable that the diatom has been around for a long time, and has started to bloom more recently, favored by locally altered conditions of the eutrophic SAO channel. This might not only result in the observed mass developments, but also can lead to a further extension of this species in the area. So far information on the expansion of bloom forming benthic marine diatoms is scarce. Studies from limnic environments, e.g. the “rock snot” *Didymosphenia geminata* (Bergey and Spaulding, 2015), which invaded New Zealand freshwater, covering wide benthic areas within short time; and first evidences for marine habitats (*Biddulphia biddulphiana*, Galland and Pennebaker, 2012)

underline the need of further investigations and study of potential spreading species.

5. Conclusion

As shown in our study *B. rutilans* plays a key role for the sedimentary coastal ecosystem. Its feasibility to grow on a wide range of substrates and to rapidly form pronounced blooms under nutrient-enriched (polluted) conditions seem to make it a suitable indicator for water quality in marine environments. Due to its observed morphological plasticity and colonization capability, *B. rutilans* can rapidly respond to changes in its environment, profiting from human driven alterations. So far hardly anything is known on the ecology and further distribution of this species within the

research area and adjacent coastal zones. Due to its ecological importance and the high probability of its expansion, further studies are urgently needed.

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