



## Diatoms associated with two South African kelp species: *Ecklonia maxima* and *Laminaria pallida*

NAS Mayombo, R Majewska & AJ Smit

To cite this article: NAS Mayombo, R Majewska & AJ Smit (2019) Diatoms associated with two South African kelp species: *Ecklonia maxima* and *Laminaria pallida*, African Journal of Marine Science, 41:2, 221-229, DOI: [10.2989/1814232X.2019.1592778](https://doi.org/10.2989/1814232X.2019.1592778)

To link to this article: <https://doi.org/10.2989/1814232X.2019.1592778>



Published online: 24 Jul 2019.



Submit your article to this journal [↗](#)



Article views: 63



View related articles [↗](#)



View Crossmark data [↗](#)



Citing articles: 6 View citing articles [↗](#)

## Short communication

# Diatoms associated with two South African kelp species: *Ecklonia maxima* and *Laminaria pallida*

NAS Mayombo<sup>1\*</sup> , R Majewska<sup>2,3</sup>  and AJ Smit<sup>1,4</sup> 

<sup>1</sup> Department of Biodiversity and Conservation Biology, University of the Western Cape, Cape Town, South Africa

<sup>2</sup> Unit for Environmental Sciences and Management, School of Biological Sciences, North-West University, Potchefstroom, South Africa

<sup>3</sup> South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, South Africa

<sup>4</sup> Elwandle Coastal Node, South African Environmental Observation Network (SAEON), Port Elizabeth, South Africa

\* Corresponding author, e-mail: [sergemayombo@yahoo.fr](mailto:sergemayombo@yahoo.fr)

Kelp forests are believed to host a large biomass of epiphytic fauna and flora, including diatoms, which constitute the base of aquatic food webs and play an important role in the transfer of energy to higher trophic levels. Epiphytic diatom assemblages associated with two common species of South African kelps, *Ecklonia maxima* and *Laminaria pallida*, were investigated in this study. Primary blades of adult and juvenile thalli of both kelp species were sampled at False Bay in July 2017 and analysed using scanning electron microscopy. Our findings showed that both kelp species hosted relatively low densities of diatoms (ranging from 7 [SD 5] cells mm<sup>-2</sup> on adult specimens of *L. pallida* to 43 [SD 66] cells mm<sup>-2</sup> on blades of juvenile *E. maxima*), with *Amphora* and *Gomphoseptatum* reaching the highest absolute abundances. Although non-metric multidimensional scaling showed overlapping and largely scattered sample sets, a significant relationship between the diatom communities and the species and age of the host macroalga was detected by two-way PERMANOVA. In general, more abundant and diverse diatom communities were observed on juvenile thalli than on adult thalli, with species belonging to *Navicula* and *Rhoicosphenia* contributing significantly to the observed dissimilarity. Due to a significant interaction between species and age effects, however, the overall ability of kelp species, their age, and their interaction to explain the variation in diatom community structure was limited. We suggest that the low densities of epiphytic diatoms were directly related to the sloughing of epithelial cells observed in both kelp species. We further speculate that on such unstable substrata some diatom taxa might adapt to an endophytic life to avoid the antifouling mechanisms developed by their hosts.

**Keywords:** Bacillariophyceae, diatom abundance, endophytic diatoms, epiphytes, False Bay, macroalgae, Phaeophyceae, seaweeds

## Introduction

Kelps, the large brown macroalgae (Phaeophyceae, Laminariales), colonise almost all temperate to polar rocky shorelines throughout the world (Arnold et al. 2016; Krumhansl et al. 2016) and constitute highly complex, dynamic and multifunctional coastal benthic ecosystems (Leclerc et al. 2016). Kelp forests provide distinct macro- and micro-habitats for numerous associated biota, which make them one of the most-productive marine environments (Steneck et al. 2002). In southern Africa, kelp forests occur from Cape Agulhas (South Africa) to Lüderitz (Namibia), within the rocky shorelines influenced by the cold waters of the Benguela upwelling system (Velimirov et al. 1977; Allen and Griffiths 1981; Bustamante and Branch 1996). *Ecklonia maxima* (Osbeck) Papenfuss and *Laminaria pallida* Greville ex. J. Agardh are the dominant kelp species in this region, with *Macrocystis angustifolia* Bory sometimes present in sheltered bays. The dynamics, composition, distribution patterns and standing crops of various macroalgal and

animal communities living within South African kelp beds have been extensively investigated and are relatively well documented (Velimirov et al. 1977; Bustamante et al. 1995; Browne et al. 2013). However, studies investigating epiphytic diatom assemblages associated with local seaweeds are sparse, with most being purely floristic surveys dating back to the 1970s (Giffen 1971, 1973, 1976). In many marine ecosystems, epiphytic diatoms, rather than the basiphyte with which they are associated, constitute the basis for much of the primary consumer productivity (Daume et al. 1997; Kasim and Mukai 2006), and in order to establish the trophic importance of diatoms in kelp ecosystems, an assessment of the diversity, abundance and distribution of these microalgae is essential.

Diatoms thrive in all aquatic, semi-aquatic, and even moderately humid or semi-arid ecosystems throughout the world, flourishing on muddy and sandy sediments, rocks, aquatic plants and animals, and all non-toxic immersed

artificial objects (Round et al. 1990; Tiffany 2011), and they are known to be sensitive and reliable bioindicators of various environmental conditions (Smol and Stoermer 2010). Species composition of sessile epiphytic diatom communities is a direct result of the particular combination of long-term environmental factors prevailing in their ecosystems. Therefore, it is likely that they could be used effectively as proxies for reconstructing past climatic conditions (Kirsten et al. 2018), and for monitoring present multidimensional changes recently detected in South African coastal waters (Schlegel et al. 2017a, 2017b).

Several studies have investigated epiphytic diatom assemblages on macroalgae in different regions across the globe (Takano 1962; Snoeijs 1994; Chung and Lee 2008; Totti et al. 2009; Majewska et al. 2013a, 2013b, 2015, 2016; Costa et al. 2014, 2016). Yet, similar reports that focus on kelp-associated diatoms are generally very scarce, descriptive, and geographically limited (Siqueiros-Beltrones et al. 2002, 2014, 2016). This article aims to provide an overview and baseline descriptions of epiphytic diatom assemblages associated with the two most common southern African kelp species, *E. maxima* and *L. pallida*, at different growth stages. It is the first report presenting and discussing local epiphytic diatom abundances and the structural and compositional differences between communities growing on adult and juvenile specimens.

## Materials and methods

### Sample collection

Kelp thalli used in this study were collected by SCUBA diving in False Bay, South Africa, east of the Cape Peninsula, around Miller's Point (34.219833° S, 18.639997° E), on 24 July 2017. The sea bottom was mainly rocky, with patches of sand present between the kelp clusters and encrusting coralline algae covering the hard surfaces. The maximum depth at the site was 10 m and the water temperature recorded *in situ* at the time of collection was 15 °C (with the maximal and minimal temperatures recorded during winter 2017 being 15.2 °C and 12.2 °C, respectively). Four juvenile (<1.5 m long) and four adult (>3 m long) specimens of each kelp species were collected. Immediately after collection, each thallus was cut, fixed in a 4% formalin solution made up with filtered seawater, and subsequently processed in the laboratories of the Department of Biodiversity and Conservation Biology at the University of the Western Cape (UWC, Cape Town, South Africa) and the Unit for Environmental Sciences and Management at North-West University (NWU, Potchefstroom, South Africa). To avoid possible biases due to differences in substrate morphology, only primary blades (the primary axis and growth zone) were chosen for further analyses. Three pieces of approximately 1 cm<sup>2</sup> of each specimen were dehydrated by immersion in ethanol solutions at increasing concentrations (30%, 50%, 60%, 70%, 80%, 90%, 95%, and absolute ethanol), followed by critical-point drying (HCP-2 critical point dryer, Hitachi, Japan), before being mounted on 13-mm aluminum stubs with adhesive carbon tape, and sputter-coated with gold/palladium (Au/Pd) using a Q150T ES (Quorum Technologies Ltd, UK) sputter coater. Diatom observation

and counting were carried out at high magnification using an Auriga field emission scanning electron microscope and a Leo 1450 scanning electron microscope (Carl Zeiss Group, Germany). Diatom cells, still attached to the dehydrated kelp thalli, were counted over a surface area of at least 1 mm<sup>2</sup> on each of the three replicates prepared.

For taxonomic identification of diatoms, two or three sections of about 2 cm<sup>2</sup> of the analysed thalli were digested with boiling concentrated nitric and sulphuric acids, at a ratio of 2:1. The resulting solutions were repetitively centrifuged and rinsed with distilled water until an approximately neutral pH was reached. The cleaned diatom material was used to prepare both permanent slides for light microscopy observations and specimen stubs for scanning electron microscopy. The slides are stored at the Department of Biodiversity and Conservation Biology, UWC. All diatom frustules were identified to at least genus level, following the available literature (e.g. Giffen 1971, 1973, 1976; Medlin and Round 1986; Witkowski et al. 2011; Lobban et al. 2012; Al-Handal et al. 2016).

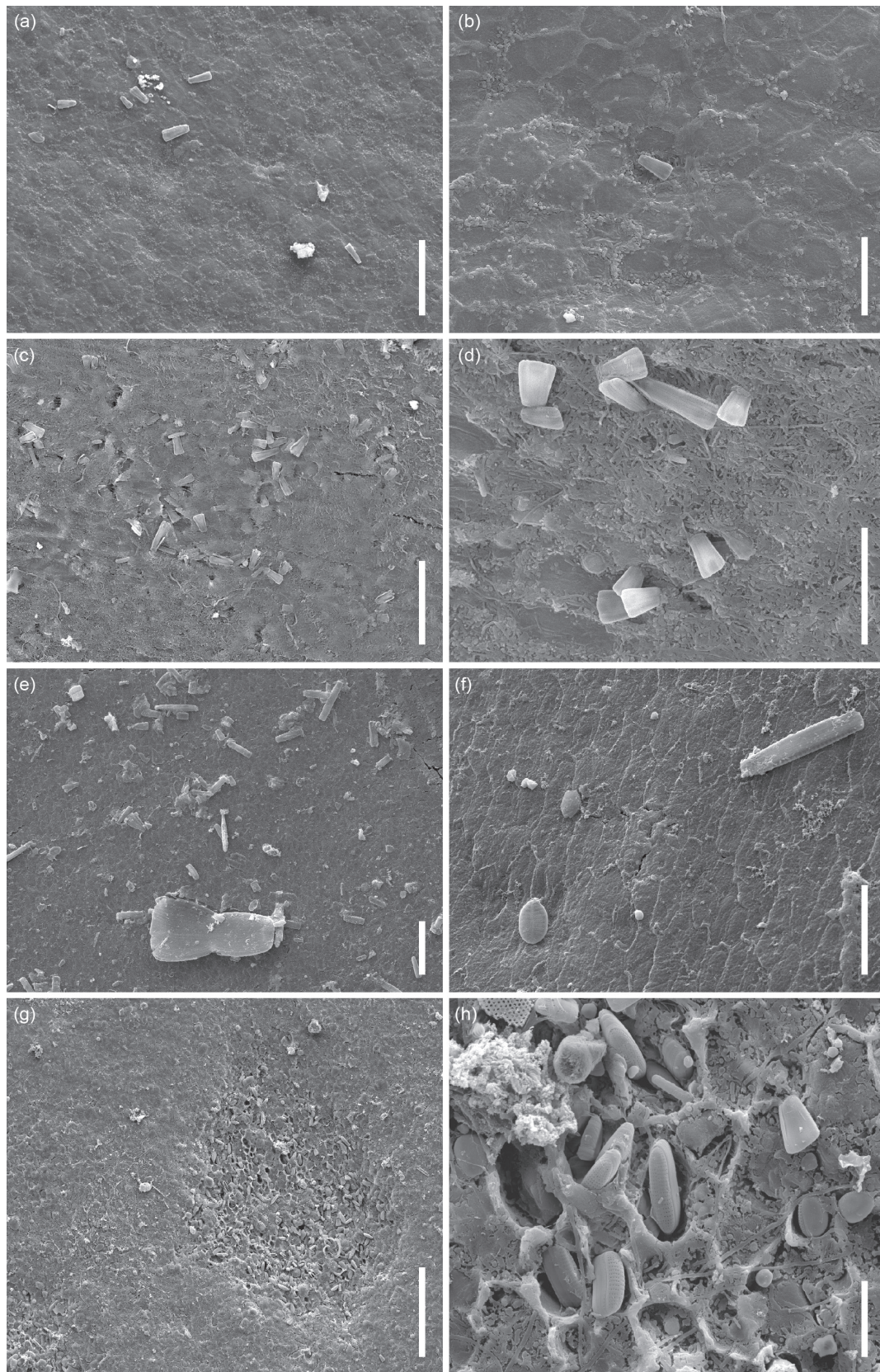
### Data analysis

All statistical analyses were performed using R 3.5.1 (R Core Team 2018), the 'vegan' package (version 2.5-3; Oksanen et al. 2018), and the 'mvabund' package (version 3.13.1; Wang et al. 2018). Species-abundance data were subjected to a logarithmic standardisation ( $\log_2 x + 1$  for  $x > 0$ , where  $x$  is the number of cells per 1 mm<sup>2</sup>), which gives less weight to taxa present at a greater abundance relative to those that are less abundant (Anderson et al. 2006). The multivariate homogeneity of group dispersions (variances) was assessed using the 'vegan' 'betadisper' function, prior to undertaking a permutational multivariate ANOVA (PERMANOVA) using the 'vegan' 'adonis2' function to test for significant differences between diatom assemblages associated with different kelp species and age groups (999 permutations for both 'betadisper' and 'adonis2'). The 'manyglm' function was used (Warton et al. 2012; Benesh and Kalbe 2016) to examine the question of which of the diatom taxa were responsible for differences in the main effects, and this was achieved by examining species one at a time (i.e. multiple univariate general linear models [GLMs]) and adjusting the *p*-values for multiple comparisons in order to minimise the chance of committing Type I errors (Wang et al. 2012). This latter approach was used instead of the well-known SIMPER analysis, which is unable to detect taxa that differ among groups because of ambiguities that stem from between-group (differences in mean) and within-group (dispersion) effects (Warton et al. 2012). Non-metric multidimensional scaling (nMDS) was then applied using the Bray–Curtis similarity index, with 999 permutations to visualise the group differences.

## Results

The SEM images of both seaweed species revealed highly homogeneous surfaces harbouring sparse diatom assemblages (Figure 1). The average diatom cell densities on *Laminaria pallida* were 7 (SD 5) cells mm<sup>-2</sup> and 38





**Figure 1:** Epiphytic diatoms associated with *Laminaria pallida* (a–d) and *Ecklonia maxima* (e–h) collected in False Bay, South Africa: (a, b) *Gomphoseptatum* sp. on the surface of an adult thallus of *L. pallida*; (c) diatoms growing on juvenile *L. pallida*; (d) *Gomphoseptatum* sp. growing on juvenile *L. pallida*; (e, f) diatoms growing on adult *E. maxima*; (g, h) diatoms dwelling in tissue of juvenile *E. maxima*. Scale bars = 10  $\mu$ m (h); 20  $\mu$ m (b, d, f); 40  $\mu$ m (e); 50  $\mu$ m (a, c); 100  $\mu$ m (g)



(SD 77) cells mm<sup>-2</sup> on adult and juvenile specimens, respectively. On *Ecklonia maxima*, average absolute diatom abundances amounted to 21 (SD 15) cells mm<sup>-2</sup> and 43 (SD 66) cells mm<sup>-2</sup> on adult and juvenile blades, respectively (Figure 2). Six subsamples, including five replicates of *L. pallida* and one of *E. maxima*, contained no epiphytic diatoms and were excluded from further analyses. In total, 18 diatom genera were found associated with the two host kelp species.

Differences in homogeneity of group dispersions were not significant for either the host species or age effects (df = 1, SS = 0.059,  $F = 2.609$ ,  $p = 0.114$  and df = 1, SS = 0.001,  $F = 0.060$ ,  $p = 0.807$ , respectively) (Figure 3a, b). The nMDS graphs showed overlapping and largely scattered sample sets (Figure 3d, e). The analysis indicated a strong correlation between the observed dissimilarity and the ordination distance ( $R^2 = 0.96$ ), with a low stress of 0.19 (Figure 3c). Given the PERMANOVA showing significant interaction between the species and age effects (df = 1, SS = 0.573,  $F = 4.544$ ,  $R^2 = 0.073$ ,  $p = 0.001$ ), a large between-plant variation interacting with kelp species and age (df = 12, SS = 3.317,  $F = 2.193$ ,  $R^2 = 0.423$ ,  $p = 0.001$ ), and the high residual variance (df = 26, SS = 3.277,  $R^2 = 0.418$ ), we find weak support for asserting that the host-kelp species or age affect diatom community structure even though the main effects were both significant (host species: df = 1, SS = 0.299,  $F = 2.373$ ,  $R^2 = 0.038$ ,  $p = 0.029$ ; age: df = 1, SS = 0.373,  $F = 2.957$ ,  $R^2 = 0.0475$ ,  $p = 0.005$ ).

Although overall diatom community structure did not differ between kelp species and age, the 'manyglm' function revealed that the abundances of seven diatom genera (*Rhoicosphenia*, *Navicula*, *Grammatophora*, *Nitzschia*, *Amphora*, *Cocconeis* and *Nagumoea*) were responsible for ~75% of the limited variance observed between the adult and juvenile thalli, with the general trend of higher diatom abundances for the juveniles. The taxa whose abundances differed significantly between adult and juvenile kelps were *Navicula* spp. (Wald = 3.66,  $p = 0.017$ ) and *Rhoicosphenia* spp. (Wald = 4.06,  $p = 0.004$ ) (Figure 4), and in both instances their number was greatest on the juvenile kelp thalli.

## Discussion

The observed epiphytic diatom abundances, ranging from 7 (SD 5) cells mm<sup>-2</sup> to 43 (SD 66) cells mm<sup>-2</sup>, were generally low, although comparable to those recorded for other seaweed species growing in various parts of the world (Snoeijs 1994; Totti et al. 2009; Majewska et al. 2013a, 2013b, 2015, 2016; Majewska and De Stefano 2015; Siqueiros-Beltrones et al. 2002, 2016; Costa et al. 2014, 2016). Totti et al. (2009) found from 7 (SD 5) to 7 524 (SD 3 491) diatom cells mm<sup>-2</sup> on 10 species of brown, red and green macroalgae from coastal waters of Iceland, with the lowest and the highest values observed on two Ochrophyta species, *Laminaria saccharina* (Linnaeus) J.V. Lamouroux and *Fucus vesiculosus* Linnaeus, respectively. Majewska et al. (2013a, 2016) recorded a mean total diatom cell density ranging from 21 (SD 13) cells mm<sup>-2</sup> to >8 000 cells mm<sup>-2</sup>

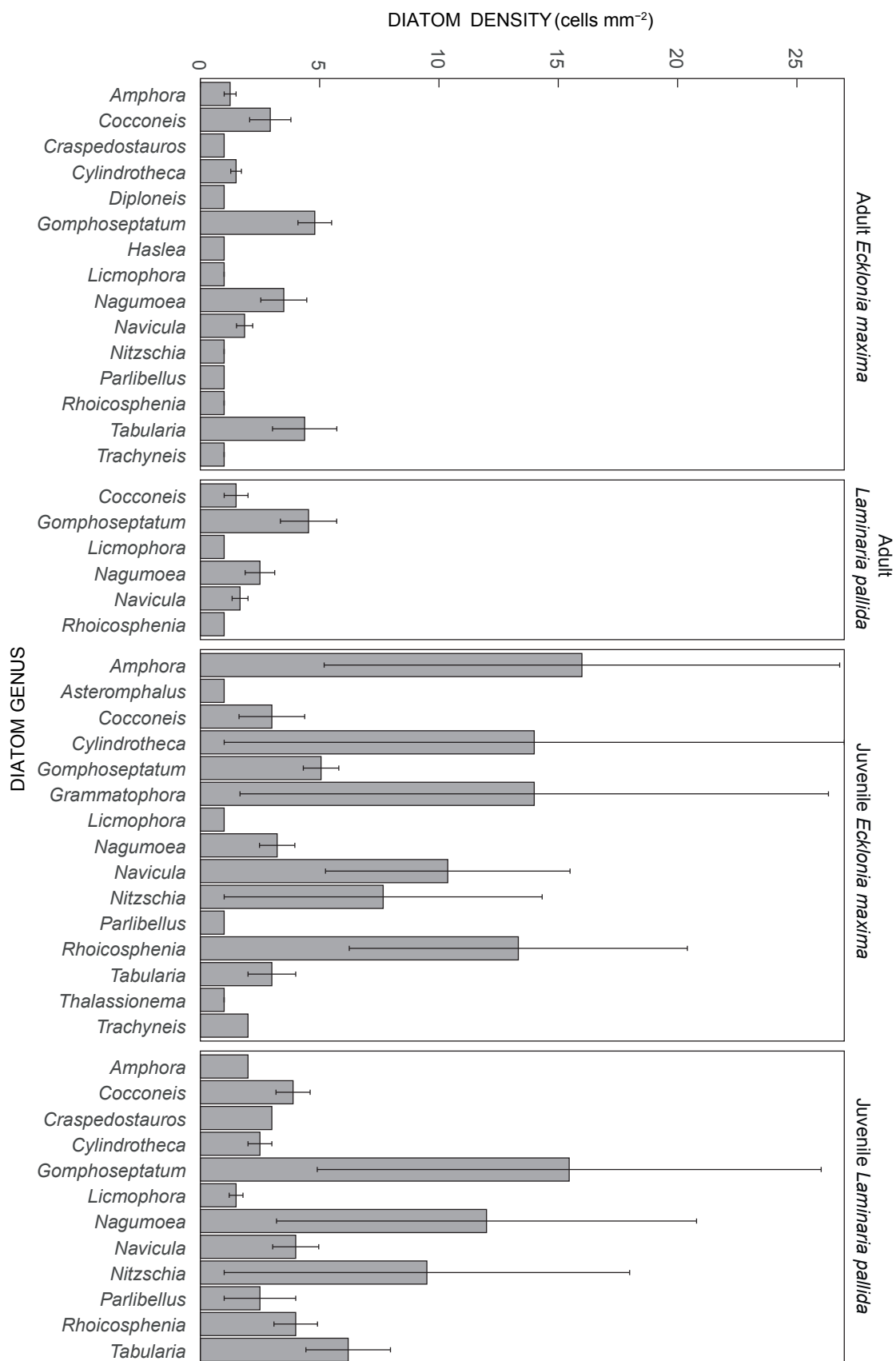
on three red algae (Rhodophyta) species from the Ross Sea (Antarctica), and from 2 951 (SD 78) cells mm<sup>-2</sup> to 10 919 (SD 2 260) cells mm<sup>-2</sup> on *Plocamium cartilagineum* (Linnaeus) P.S. Dixon (Rhodophyta) from Admiralty Bay (King George Island, Antarctica; Majewska et al. 2015). Thomas and Jiang (1986), who analysed 15 species of brown, red and green macroalgae from another Antarctic region (Prydz Bay), reported that ubiquitous *Cocconeis* spp. reached densities approaching 105 cells cm<sup>-2</sup> (i.e. ~1 000 cells mm<sup>-2</sup>), whereas *Nitzschia* spp. were twice as abundant.

Similarly, the number of diatom genera (18) found growing epiphytically on the examined blades of *Ecklonia maxima* and *Laminaria pallida* was relatively low, suggesting low diatom diversity. Totti et al. (2009) found 19 diatom genera in seaweed samples from Reykjanes Peninsula (Iceland), whereas Majewska et al. (2016) observed 44 diatom genera associated with rhodophytes from the Ross Sea and 21 associated with *P. cartilagineum* from Admiralty Bay. Al-Handal and Wulff (2008) recorded 29 diatom genera in samples of 19 seaweed species from Potter Cove (Antarctica), with 11 genera present in samples of seven Phaeophyceae species. Furthermore, 29 diatom genera were found in an analysis of three seaweed species from northeastern Brazil (Costa et al. 2016).

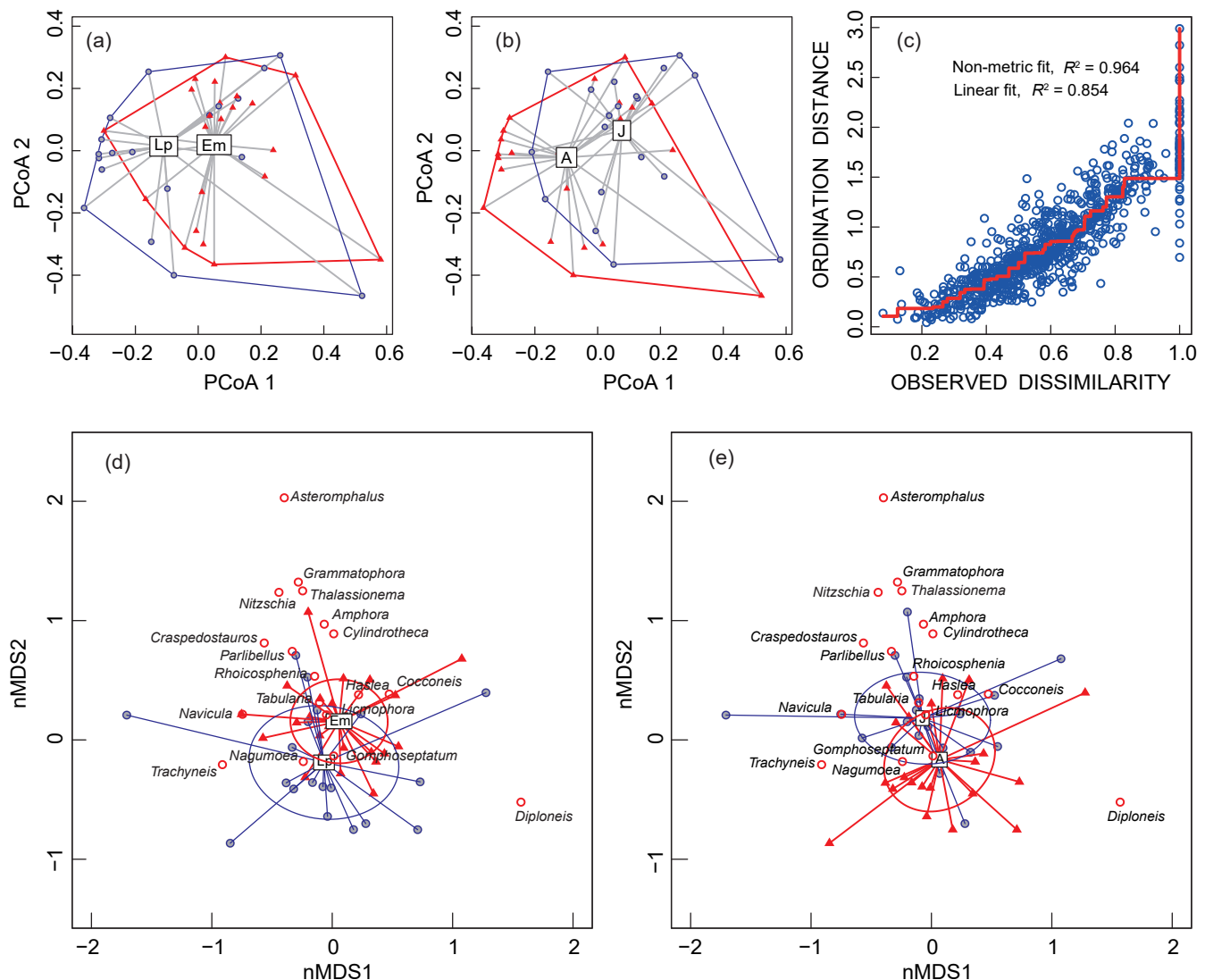
It was suggested (Majewska et al. 2013a, 2013b, 2016; Costa et al. 2016) that macroalgal thalli with highly homogeneous surfaces (micro-topography) and uniform morphology, as in both *E. maxima* and *L. pallida*, would host less-diverse epiphytic diatom communities due to high competition among epiphytic organisms with overlapping niches. This may partly explain the low numbers of diatom taxa found in the present study. Nevertheless, it does not explain the very low diatom abundances.

Seaweeds, including brown macroalgae, defend themselves against both biofouling and grazers using a range of strategies (Hellio et al. 2001; Yamamoto et al. 2013). These may involve secretion of chemically active metabolites, which act as antifouling or repelling agents (Kubanek et al. 2003; Wikström and Pavia 2004), or shedding of the outer layer of the thallus (epithallus) (Moss 1982; Yamamoto et al. 2013; Halat et al. 2015). The SEM observations confirmed that surface-cell sloughing occurs in both kelp species examined and appears to be a particularly efficient antifouling mechanism. We speculate that this mechanical defence against surface colonisation is one of the major factors that affect epiphytic diatom communities, preventing their development into the climax stage, which would explain the observed low similarity levels within the examined groups of samples (classified according to the host seaweed species and age) and would obscure the patterns and differences in diatom composition detected between the groups.

However, despite the apparently highly successful antifouling strategies employed by both kelp species, we found indications of endophytic diatom growth in areas of presumably damaged or growing surface tissue and natural superficial breaks (Russell and Veltkamp 1984). This phenomenon was described by Klochkova et al. (2014), who found an unknown endophytic species of *Pseudogomphonema* (Naviculaceae, Bacillariophyceae),



**Figure 2:** Mean abundances of diatom taxa on adult and juvenile thalli of *Ecklonia maxima* and *Laminaria pallida* sampled in False Bay, South Africa, July 2017. Error bars represent standard error (SE)



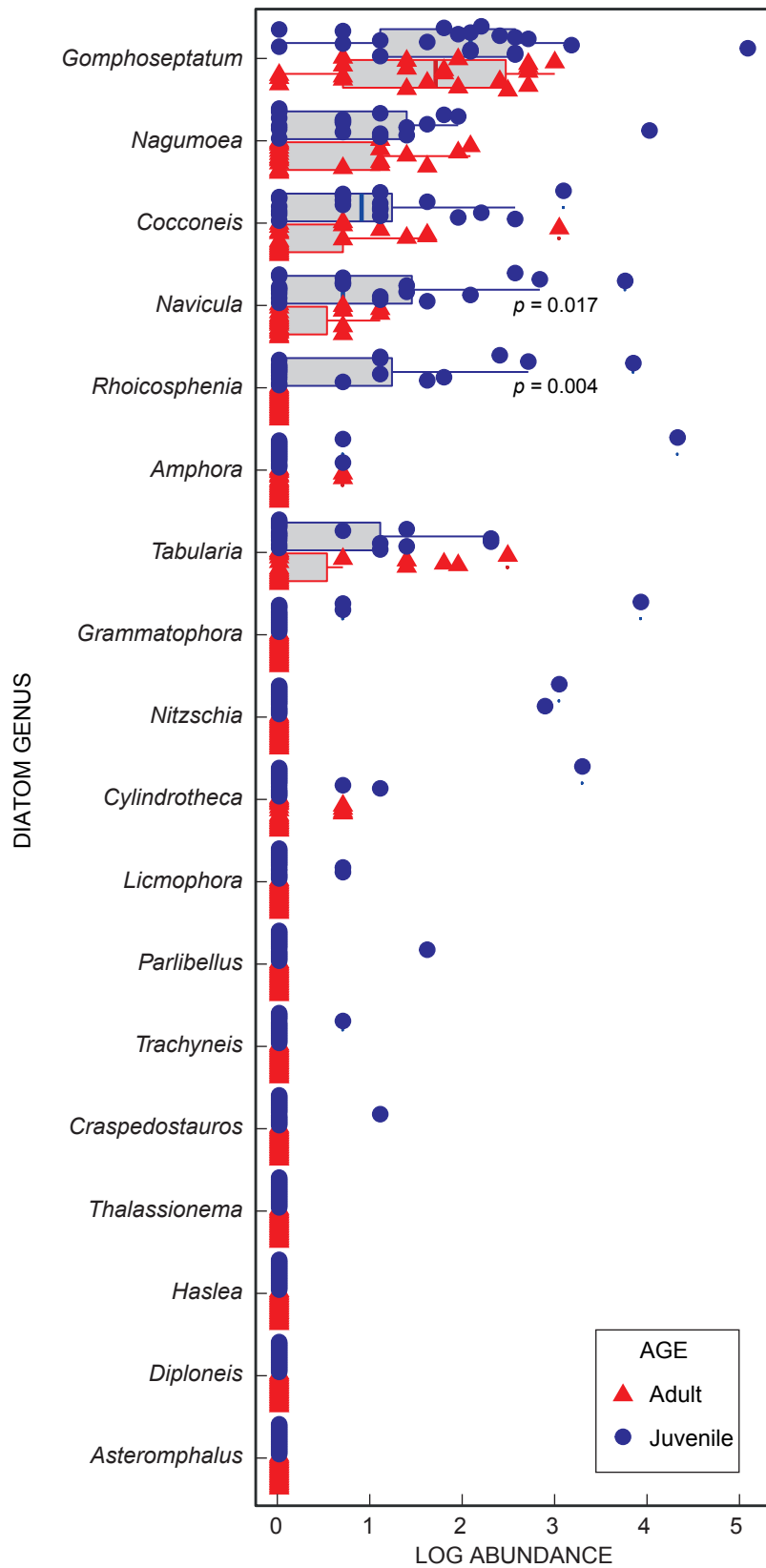
**Figure 3:** Unconstrained ordination diagrams. Plots produced by principal coordinates analysis (PCoA), showing the diatom assemblages on the two host species of kelp (a) and by host age (b). (c) Shepard plot of the non-metric multidimensional scaling (nMDS) results. nMDS graphs based on diatom taxa abundances, showing the relationship between the diatom communities growing on both host species (d) and by host age (e). A = adult; J = juvenile; Em = *Ecklonia maxima*; Lp = *Laminaria pallida*

which was reproducing within the medullar layer of the host alga thallus, to be responsible for significant and widespread tissue damage in the red alga *Neoabbottiella* Perestenko (Halymeniaceae, Rhodophyta). Species of endophytic diatoms were previously described by Hasle (1968), who found *Navicula endophytica* living in the intercellular substance of *Ascophyllum nodosum* (L.) Le Jolis (Ochrophyta), and by Okamoto et al. (2003), who described *Gyrosigma coelophilum* from thalli of *Coelarthrum opuntia* (Endlicher) Børgesen (Rhodophyta). Although all aspects of diatom endobiosis are either very poorly studied or unknown, this kind of survival strategy and development mode may be not uncommon in marine habitats.

According to the results of the current study, epiphytic diatom communities were influenced by their hosts' age,

with generally both more abundant and diverse diatom communities found on juvenile thalli, whereas the species of algal host seemed to be of less importance. Nevertheless, due to a significant interaction between the two factors tested, the overall ability of both kelp age and species to explain the variation in diatom community structure was low. Future investigations will aim to determine whether the same patterns prevail on other parts of the kelp thallus, such as the secondary blade, stipe and holdfast.

**Acknowledgements** — We thank our colleagues from the Team Kelp (UWC) for assisting with the sample collection and Łukasz Polanski for editing the figures. This study was supported by the South African National Research Foundation (NRF) through the South African Institute for Aquatic Biodiversity's ACEP Phuhlisla Programme.



**Figure 4:** Univariate generalised linear models fitted individually to each diatom taxon found on adult and juvenile thalli of the kelps collected in False Bay, South Africa; small dots beneath some data points denote outliers



## ORCID

Roysana Majewska  <https://orcid.org/0000-0003-2681-4304>

Ntambwe Albert Serge Mayombo  <https://orcid.org/0000-0001-6418-1419>

Albertus J Smit  <https://orcid.org/0000-0002-3799-6126>

## References

- Al-Handal A, Wulff A. 2008. Marine epiphytic diatoms from the shallow sublittoral zone in Potter Cove, King George Island, Antarctica. *Botanica Marina* 51: 411–435.
- Al-Handal AY, Compère P, Riaux-Gobin C. 2016. Marine benthic diatoms in the coral reefs of Reunion and Rodrigues Islands, West Indian Ocean. *Micronesica* 3: 1–77.
- Allen JC, Griffiths CL. 1981. The fauna and flora of a kelp-bed canopy. *Journal of Zoology* 16: 80–84.
- Anderson MJ, Ellingsen KE, McArdle BH. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9: 683–693.
- Arnold M, Teagle H, Brown MP, Smale DA. 2016. The structure of biogenic habitat and epibiotic assemblages associated with the global invasive kelp *Undaria pinnatifida* in comparison to native macroalgae. *Biological Invasions* 18: 661–676.
- Benesh DP, Kalbe M. 2016. Experimental parasite community ecology: intraspecific variation in a large tapeworm affects community assembly. *Journal of Animal Ecology* 85: 1004–1013.
- Browne CM, Milne R, Griffiths C, Bolton JJ, Anderson RJ. 2013. Epiphytic seaweeds and invertebrates associated with South African populations of the rocky shore seagrass *Thalassodendron leptocaula* – a hidden wealth of biodiversity. *African Journal of Marine Science* 35: 523–531.
- Bustamante RH, Branch GM. 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. *Journal of Experimental Marine Biology and Ecology* 196: 1–28.
- Bustamante RH, Branch GM, Eekhout S. 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology* 76: 2314–2329.
- Chung MH, Lee KS. 2008. Species composition of the epiphytic diatoms on the leaf tissues of three *Zostera* species distributed on the southern coast of Korea. *Algae* 23: 75–81.
- Costa MMDS, Pereira SMB, De Arruda PC, Leca EE. 2014. Quantitative variation of epiphytic diatoms in *Galaxaura rugosa* (Nemaliales: Rhodophyta). *Marine Biodiversity Records* 7: 1–7.
- Costa MMDS, Pereira SMB, Da Silva-Cunha MDGG, De Arruda PC, Eskinazi-Leça E. 2016. Community structure of epiphytic diatoms on seaweeds in northeastern Brazil. *Botanica Marina* 59: 231–240.
- Daume S, Brand S, Woelkerling WJ. 1997. Effects of post-larval abalone (*Haliotis rubra*) grazing on the epiphytic diatom assemblage of coralline red algae. *Molluscan Research* 18: 119–130.
- Giffen MH. 1971. Marine littoral diatoms from the Gordon's Bay region of False Bay, Cape Province, South Africa. *Botanica Marina* 14: 1–16.
- Giffen MH. 1973. Diatoms of the marine littoral of Steenberg's Cove in St Helena Bay, Cape Province, South Africa. *Botanica Marina* 16: 32–48.
- Giffen MH. 1976. A further account of the marine littoral diatoms of the Saldanha Bay Lagoon, Cape Province, South Africa. *Botanica Marina* 19: 379–394.
- Halat L, Galway ME, Gitto S, Garbary DJ. 2015. Epidermal shedding in *Ascophyllum nodosum* (Phaeophyceae): seasonality, productivity and relationship to harvesting. *Phycologia* 54: 599–608.
- Hasle GR. 1968. *Navicula endophytica* sp. nov., a pennate diatom with an unusual mode of existence. *British Phycological Bulletin* 3: 475–480.
- Hellio C, Thomas-Guyon H, Culioli G, Piovetti L, Bourgougnon N, Le Gal Y. 2001. Marine antifoulants from *Bifurcaria bifurcata* (Phaeophyceae, Cystoseiraceae) and other brown macroalgae. *Biofouling* 17: 189–201.
- Kasim M, Mukai H. 2006. Contribution of benthic and epiphytic diatoms to clam and oyster production in the Akkeshi-ko estuary. *Journal of Oceanography* 62: 267–281.
- Kirsten KL, Habertzettl T, Wüdsch M, Frenzel P, Meschner S, Smit AJ et al. 2018. A multiproxy study of the ocean-atmospheric forcing and the impact of sea-level changes on the southern Cape coast, South Africa, during the Holocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 496: 282–291.
- Klochkova TA, Pisareva NA, Park JS, Lee JH, Han JW, Klochkova NG, Kim GH. 2014. An endophytic diatom, *Pseudogomphonema* sp. (Naviculaceae, Bacillariophyceae), lives inside the red alga *Neobabbottella* (Halymeniaceae, Rhodophyta). *Phycologia* 53: 205–214.
- Krumhansl KA, Okamoto DK, Rassweiler A, Novak M, Bolton JJ, Cavanaugh KC et al. 2016. Global patterns of kelp forest change over the past half-century. *Proceedings of the National Academy of Sciences of the United States of America* 113: 13785–13790.
- Kubanek J, Jensen PR, Keifer PA, Sullards MC, Collins DO, Fenical W. 2003. Seaweed resistance to microbial attack: a targeted chemical defense against marine fungi. *Proceedings of the National Academy of Sciences of the United States of America* 100: 6916–6921.
- Lobban CS, Scheffter M, Jordan RW, Arai Y, Sasaki A, Theriot EC et al. 2012. Coral-reef diatoms (Bacillariophyta) from Guam: new records and preliminary checklist, with emphasis on epiphytic species from farmer-fish territories. *Micronesica* 43: 237–479.
- Leclerc JC, Riera P, Lévêque L, Davoult D. 2016. Contrasting temporal variation in habitat complexity and species abundance distributions in four kelp forest strata. *Hydrobiologia* 777: 1–22.
- Majewska R, De Stefano M. 2015. Epiphytic diatom communities on *Phyllophora antarctica* from the Ross Sea. *Antarctic Science* 27: 44–56.
- Majewska R, Gambi MC, Totti CM, Pennesi C, De Stefano M. 2013a. Growth-form analysis of epiphytic diatom communities of Terra Nova Bay (Ross Sea, Antarctica). *Polar Biology* 36: 73–86.
- Majewska R, Gambi MC, Totti CM, De Stefano M. 2013b. Epiphytic diatom communities of Terra Nova Bay, Ross Sea, Antarctica: structural analysis and relations to algal host. *Antarctic Science* 25: 501–513.
- Majewska R, Kuklinski P, Balazy P, Yokoya NS, Martins AP, De Stefano M. 2015. A comparison of epiphytic diatom communities on *Plocamium cartilagineum* (Plocamiales, Florideophyceae) from two Antarctic areas. *Polar Biology* 38: 189–205.
- Majewska R, Convey P, De Stefano M. 2016. Summer epiphytic diatoms from Terra Nova Bay and Cape Evans (Ross Sea, Antarctica) – a synthesis and final conclusions. *PLoS ONE* 11: e0153254.
- Medlin LK, Round FE. 1986. Taxonomic studies of marine gomphonemoid diatoms. *Diatom Research* 1: 205–225.
- Moss BL. 1982. The control of epiphytes by *Halidrys siliquosa* (L.) Lyngb. (Phaeophyta, Cystoseiraceae). *Phycologia* 21: 185–191.
- Okamoto N, Nagumo T, Tanaka J, Inouye I. 2003. An endophytic diatom *Gyrosigma coelophilum* sp. nov. (Naviculales, Bacillariophyceae) lives inside the red alga *Coelarthrum opuntia* (Rhodmeliales, Rhodophyceae). *Phycologia* 42: 498–505.
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGinn D et al. 2018. *vegan: community ecology package*. R package version 2.5-3.
- R Core Team. 2018. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

- Round FE, Crawford RM, Mann DG. 1990. *Diatoms: biology and morphology of the genera*. Cambridge, UK: Cambridge University Press.
- Russel G, Veltkamp CJ. 1984. Epiphyte survival on skin-shedding macrophytes. *Marine Ecology Progress Series* 18: 149–153.
- Schlegel RW, Oliver ECJ, Perkins-Kirkpatrick S, Kruger A, Smit AJ. 2017a. Predominant atmospheric and oceanic patterns during coastal marine heatwaves. *Frontiers in Marine Science* 4: article 323.
- Schlegel RW, Oliver ECJ, Wernberg T, Smit AJ. 2017b. Nearshore and offshore co-occurrence of marine heatwaves and cold-spells. *Progress in Oceanography* 151: 189–205.
- Siqueiros-Beltrones DA, Argumedo-Hernández U. 2014. Quasi-monospecific proliferation of *Pteroncola inane* (Giffen) Round (Fragilariiales; Bacillariophyceae) on blades of *Eisenia arborea* Areschoug. *CICIMAR Oceanides* 29: 57–62.
- Siqueiros-Beltrones DA, Serviere-Zaragoza E, Hernandez UA. 2002. Epiphytic diatoms of *Macrocytis pyrifera* (L.) C. Ag. from the Baja California Peninsula, México. *Oceanides* 17: 3–39.
- Siqueiros-Beltrones DA, Argumedo-Hernandez U, Landa-Cansigno C. 2016. Uncommon species-diversity values in epiphytic diatom assemblages of the kelp *Eisenia arborea*. *Hidrobiologica* 26: 61–76.
- Smol JP, Stoermer EF. 2010. *The diatoms: applications for the environmental and earth sciences* (2nd edn). Cambridge, UK: Cambridge University Press.
- Snoeijs P. 1994. Distribution of epiphytic diatom species composition, diversity and biomass on different macroalgal hosts along seasonal and salinity gradients in the Baltic Sea. *Diatom Research* 9: 189–211.
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* 29: 436–459.
- Takano H. 1962. Notes on epiphytic diatoms upon seaweeds from Japan. *Journal of the Oceanographical Society of Japan* 18: 29–33.
- Thomas DP, Jiang J. 1986. Epiphytic diatoms of the inshore marine area near Davis Station. *Hydrobiologia* 140: 193–198.
- Tiffany MA. 2011. Epizoic and epiphytic diatoms. In: Seckbach J, Kociolek P (eds), *The diatom world*. Dordrecht, The Netherlands: Springer Netherlands. pp 195–209.
- Totti C, Poulin M, Romagnoli T, Perrone C, Pennesi C, De Stefano M. 2009. Epiphytic diatom communities on intertidal seaweeds from Iceland. *Polar Biology* 32: 1681–1691.
- Velimirov B, Field JG, Griffiths CL, Zoutendyk P. 1977. The ecology of kelp-bed communities in the Benguela upwelling system – analysis of biomass and spatial distribution. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 30: 495–518.
- Wang Y, Naumann U, Wright ST, Warton DI. 2012. mvabund – an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution* 3: 471–474.
- Wang Y, Naumann U, Eddelbuettel D, Warton D. 2018. *mvabund: statistical methods for analysing multivariate abundance data*. R package version 3.13.1.
- Warton DI, Wright ST, Wang Y. 2012. Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution* 3: 89–101.
- Wikström SA, Pavia H. 2004. Chemical settlement inhibition versus post-settlement mortality as an explanation for differential fouling of two congeneric seaweeds. *Oecologia* 138: 223–230.
- Witkowski A, Kociolek JP, Kurzydowski KJ. 2011. Valve ultrastructure of two new genera of marine canal-bearing diatoms (Bacillariophyceae). *Phycologia* 50: 170–181.
- Yamamoto K, Endo H, Yoshikawa S, Ohkia K, Kamiya M. 2013. Various defense ability of four sargassacean algae against the red algal epiphyte *Neosiphonia harveyi* in Wakasa Bay, Japan. *Aquatic Botany* 105: 11–17.