**Distribution patterns of intertidal oribatid mites (Acari, Oribatida) from South African shores and their relationship to temperature**

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A faunistic study of the intertidal oribatid mite fauna of South Africa’s coastline revealed the presence of four species from three families, showing specific biogeographic patterns. Their occurrences show a clear east–west divide, with a small gap near East London between the Podacaridae and the other two families, the Selenoribatidae and Fortuyniidae, clearly coinciding with suggested marine biogeographic ecoregions. The podacarid Halozetes capensis is confined to the cooler warm-temperate Agulhas Ecoregion; the fortuyniid Fortuynia elamellata micromorpha and the selenoribatid Schusteria ugraseni to the warmer subtropical Natal Ecoregion; and the selenoribatid Selenoribates divergens to the tropical Delagoa Ecoregion. These distributions are an indication that the oceanic climate may be the primary factor shaping their biogeography, particularly the seawater temperatures along the coast, which are in turn affected by the Agulhas and the Benguela currents. A mean monthly sea surface temperature of approximately 22 °C apparently represents the climatic border of the distributions, with the podacarid persisting only below this temperature, and the fortuyniid and selenoribatids only above it. Global warming will certainly change these geographic ranges, and in South Africa the warm-adapted fortuyniid and selenoribatids can be expected to expand their distributions southwards, while the occurrence of the cold-adapted podacarid might be reduced to a few southwestern coastal areas in the next few decades.

**Keywords:** Agulhas Current, Ameronothroidea, Benguela Current, biogeography, global warming, littoral environment

**Online supplementary material:** The sampling locations, showing oribatid mite occurrences and their respective ecological data, are detailed in Supplementary Table S1, available at https://doi.org/10.2989/1814232X.2021.1912825.

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**Introduction**

South Africa’s shoreline stretches a distance of approximately 3 650 km, encompassing diverse terrestrial climates. The terrestrial climate in South Africa is characterised by decreasing aridity in a west to east plane (Mansell and Erasmus 2002; Mucina et al. 2006). The west coast ranges from cold desert to cold semi-arid climate, with low annual rainfall, ranging from 567 mm at Cape Agulhas at the southern end to 45 mm at Alexander Bay in the north; the south coast has a semi-arid, oceanic warm-temperate climate; and the east coast has a humid subtropical climate, with rainfall ranging from 800 mm in southern areas to 1 300 mm at the Mozambique border. The coastline shows various geologies, including sandy beaches and rocky shores, consisting of sandstone, mudstone, granites and shales (Mucina et al. 2006). Furthermore, the inland vegetation along the South African coastline includes two important biodiversity regions: the species-rich Cape Floristic Region (comprising fynbos vegetation) along the southwestern and south coasts, and the second-most-species-rich Maputaland–Pondoland–Albany hotspot found along the east coast (Cox 2001; Perera et al. 2011).

As for the coastal climate, the west coast is dominated by the upwelled cold Benguela Current that slowly drifts northwards, and the east coast is strongly influenced by the warm, rapidly southward-moving Agulhas Current (Brown and Jarman 1978; Shannon 1985). Three major biogeographic regions have been proposed for South Africa’s coast: a cold-temperate west coast province; a warm-temperate south coast province; and a subtropical east coast province (Stephenson and Stephenson 1972). Despite some discrepancies regarding the boundaries and overlap zones, these three biogeographic provinces have been established for a variety of taxonomic groups of intertidal invertebrates, coastal fishes and seaweeds (Field and Griffiths 1991; Emanuel et al. 1992; Stegenga and Bolton 1992; Bustamante and Branch 1996; Turpie et al. 2000). In a recent publication providing a national biodiversity assessment (Sink et al. 2012; also see Spalding et al. 2007), these biogeographic provinces were slightly modified and renamed as follows: the cold-temperate west coast is now called the Southern Benguela Ecoregion; the warm-temperate south coast is the Agulhas Ecoregion; and the subtropical east coast is the Natal Ecoregion. Among intertidal invertebrates, mites (of subclass Acari) represent the smallest organisms, but even for these tiny animals the
South African biogeographic pattern apparently remains intact (Procheş and Marshall 2002).

Presently, 82 species of marine-associated mites representing 33 genera are known from South African coasts, of which the majority belong to the Halacaridae, and only 12 species to the Ameronothroidea and Hyadesiidae (Procheş and Marshall 2002). The Halacaridae are the oldest known extant animal lineage that secondarily invaded the sea and can be found from the wave-splash zone to deep-sea trenches, and represent truly aquatic animals. In contrast, the Hyadesiidae and Ameronothroidea constitute considerably younger radiations and are restricted to the intertidal environment (Pepato et al. 2018), representing only semi-aquatic taxa.

From a biogeographic perspective, the Ameronothroidea are perhaps the most interesting group because the distributions of its four marine-associated families apparently correlate with climate (Procheş and Marshall 2001; Pfingstl and Schuster 2014). The Ameronothroidea and Podacaridae are mainly contained within cold-temperate regions around both poles (Procheş and Marshall 2001), with the former restricted to the Northern Hemisphere, and the latter to the Southern Hemisphere. The Fortuyniidae and Selenoribatidae are limited to shorelines of the subtropics and tropics (Pfingstl and Schuster 2014). On a global scale, there are no overlaps of supposedly cold-adapted and warm-adapted families, except for the co-occurrence of single ameronothroid and selenoribatid species in the Mediterranean Region (Pfingstl and Schuster 2014). Apart from this exception, South Africa’s coast is the only region in the world, as so far known, where cold-adapted and warm-adapted ameronothroid families are known to occur in more-or-less close geographical vicinities.

Previously, the podacarid Halozetes capensis was reported from the cold-temperate west coast and the warm-temperate south coast (Procheş and Marshall 2002; Coetzee and Marshall 2003), and the fortuyniid Fortuynia elamellata micromorpha and the selenoribatid Schustenia ugraseni were found on the subtropical east coast (Marshall and Pugh 2000; 2002; Procheş and Marshall 2002). Although these distributions appear to relate to present-day temperatures (Procheş and Marshall 2002), it remains unclear whether aerial or oceanographic climate is the dominant factor and why neighbouring occurrences are limited to the South African coastline.

Intertidal mites are subjected to air and water temperatures each day, and these temperatures may diverge markedly. Procheş et al. (2001) investigated arthropod assemblages on mangrove pneumatophores in southeastern Africa, including mites, and stated that terrestrial seasonal patterns have a greater influence than seawater temperatures. Other authors (Pfingstl and Schuster 2014; Pfingstl et al. 2019) suggested that the temperatures of large ocean currents may shape distributional patterns of, at least, the Ameronothroidea considerably. However, specific studies correlating climate and the distributions of ameronothroid mites are lacking, mainly because geographic areas with neighbouring occurrences and clear distributional borders are extremely scarce. South Africa represents such a unique study area, and the pioneering work of Procheş and Marshall (2002) provides an excellent database for studying the factors controlling the distribution of the intertidal oribatid mites of this area.

The aims of the present study were to: (i) complement the known distributions of South African Ameronothroidea; (ii) verify whether their biogeographic patterns are in accordance with postulated coastal ecoregions; (iii) combine their determined distributions with comprehensive climatic temperature data for assessing possible correlations; (iv) discuss the findings regarding their significance in view of global warming; and (v) provide a database of these taxa as a baseline for future monitoring studies.

Materials and methods

Sampling activities on South African coasts were performed from February to March in 2019 and 2020. Samples of lichen, intertidal algae, barnacles and mussel shells were scraped off rocks with a knife or a small shovel, mostly during low tide. (Additionally, coastal plant material was collected in the supralittoral area, but this material yielded none of the marine-associated focal taxa.) Samples were taken at 23 different locations that are evenly distributed over the complete South African coastline and that cover all relevant climate regions of this geographic area. At each site, 3 to 10 samples were taken (depending on availability) to obtain a good overview of the oribatid mite fauna present at the location. In addition, the pH of seawater, humidity of the air, and temperature of both the seawater and air were recorded—pH with a RoHS-compliant PH-009tA Pen Type pH Meter, and temperature and humidity with an Alia France™ Biotemp™ In/Out Thermo-Hygrometer. Temperature data taken at the locations represent snapshots and thus were not used for biogeographic consideration, but instead were used only to check whether the spot temperature lay in the range of annual climate data recorded by the government-maintained weather stations. This allowed us to check for any bias caused by possible local anomalies (which was not the case). Annual climate data (air temperature) for the last 10 years (2010–2019) were obtained from the South African Weather Service (https://www.weatherza.co.za) and annual sea surface temperatures (SST) for the year 2019 were taken from https://www.SeaTemperature.org for each site or for the next nearest location if data were not available for a given site.

Mobile Berlese-Tullgren funnels were used in a temporary field laboratory for the extraction of mites. Mites were collected alive in small plastic vessels lined with plaster of Paris, sorted with a fine brush and preserved in absolute ethanol. Specimens were embedded in Berlese mountant for microscopic examination under transmitted light (Olympus BH2 microscope) and subsequent taxonomic identification. Finally, for photographic documentation, specimens were air-dried and photographed with a Keyence VHX-5000 digital microscope.

Earlier records of focal taxa were taken from the literature (i.e. Marshall and Pugh 2000, 2002; Procheş and Marshall 2002; Coetzee and Marshall 2003) and were included in this study to infer more-complete distributional ranges of the respective families. The species mentioned in those publications and given in the present study are the same; there has been no taxonomic change.
Results
Species occurrences and distribution ranges
Four different species of intertidal oribatid mites were found at 13 of the 23 sampling locations along the South African coast (Table 1). The species were identified as: *Halozetes capensis* Coetzee and Marshall, 2003; *Fortuynia elamellata micromorpha* Marshall and Pugh, 2002; *Schusteria ugraseni* Marshall and Pugh, 2000; and *Selenoribates divergens* Pfingstl, 2015 (Figure 1). As these four species belong to families with supposedly different climate preferences, they are hereafter mostly referred to by their family designation (Podacaridae: *H. capensis*; Fortuyniidae: *F. elamellata micromorpha*; Selenoribatidae: *Schusteria ugraseni* and *Selenoribates divergens*).

Occurrences of the podacarid, fortuyniid and selenoribatids showed a clear east–west divide, with a small gap between the podacarid and the other two families (Figure 2). The podacarid, *H. capensis*, was found in the warm-temperate Agulhas Ecoregion at De Hoop Nature Reserve, in the Kaaimans River estuary near the small cove of Victoria Bay, at Nature’s Valley near Plettenberg Bay, and on Kayser’s Beach near East London. Earlier surveys (Procheş and Marshall 2002; Coetzee and Marshall 2003) showed the westernmost record of this species at Kommetjie (near Cape Point) and the easternmost record at Port Alfred. The most-western distributional limit remains, but the most-eastern limit is now at Kayser’s Beach, about 80 km east of Port Alfred. The fortuyniid *F. elamellata micromorpha* and the selenoribatid *S. ugraseni* were mostly found sympatrically at locations in the subtropical Natal Ecoregion, at Port St Johns, Port Edward, Umkomaas, Salt Rock and Umdloti (near Durban), but *S. ugraseni* was also found at Winterstrand near East London, representing the most-southwestern record for this selenoribatid. *Selenoribates divergens* was collected only at Mission Rocks near St Lucia (Delagoa Ecoregion), which represents the most-northeastern sample site in this study. Almost all positive sample locations yielded a high abundance of mites, indicating natural occurrences with stable populations.

Environmental factors
Annual SST within the distribution area of the podacarid *H. capensis* ranged from an absolute minimum of 16.4 °C to an absolute maximum of 24.5 °C, with annual mean values ranging from 17.8 to 22.7 °C (Table 1). West of Cape Point, where the mean minimum water temperature can drop below 16 °C, no occurrence of any intertidal oribatid mite was detected (Figure 3), although there is a historical record from Kommetjie, which is west of Cape Point. Annual air temperatures in areas with *H. capensis* occurrences ranged from 10.5 to 24.1 °C, with annual SST mean values ranging from 15.4 to 19.4 °C. West of Cape Point the SST mean values were slightly lower but still overlapped at 14.3–16.3 °C. The highest annual SST for locations with *H. capensis* were recorded at East London, with a range of 21.3–24.5 °C (Table 1).

In the distribution range of the fortuyniid and selenoribatids, annual SST ranged from 21.3 to 25.7 °C, with annual mean values of 22.7–24.4 °C (Table 1; Figure 3). Annual air temperatures ranged from 14.7 to 27.8 °C, with annual means of 19.4–21.3 °C. The location with the lowest SST and air temperatures was East London, and the location with the highest respective temperatures was St Lucia.

Apart from the temperature data, which were taken from meteorological and oceanographic research databases, the pH of seawater and the humidity of air were measured in the field in February at each sampling site. The pH level was quite constant along the whole South African coast, ranging from 7.7 to 8.5, with values dropping below 8.0 only west of Cape Point. In the oceanic and the humid subtropical areas with occurrences of the fortuyniid and selenoribatids, humidity was also consistent, at 70–96% (Table 1). In the warm-temperate Agulhas Ecoregion, where *H. capensis* occurs, the humidity showed much variation, ranging from 46% to 88%.

Ecological factors
The podacarid, fortuyniid and selenoribatids were all exclusively found on rocky shores. They all occurred across different zones, from the lower eulittoral to the upper eulittoral, with more than half of the *H. capensis* populations inhabiting the median to upper eulittoral, and most of the fortuyniid and selenoribatid populations found in the lower to median eulittoral areas (Supplementary Table S1).

*Halozetes capensis* occurred almost exclusively in dense patches of the marine red alga *Bostrychia intricata* and the green alga *Rhizoclonium riparium* growing in crevices or other protected areas on the intertidal rocks. The fortuyniid and selenoribatids occurred in patches of the red alga *Gelidium* sp. growing on barnacles, tubeworm colonies or mussels in the lower to median eulittoral, and in patches of *Bostrychia* sp. growing in rock crevices in the median to upper eulittoral zone.

Discussion
Distributional ranges
The findings of our study are mostly consistent with the distributional patterns suggested by Procheş and Marshall (2002) and the same species of oribatid mites were detected. However, some gaps could be filled in, and the ranges of single species are demonstrated to be considerably more extensive than formerly known. Prior to this investigation there was a single record of *F. elamellata micromorpha* from Park Rynie in KwaZulu-Natal (Marshall and Pugh 2002), but, based on the present data, a distribution from Port St Johns (Eastern Cape) to Durban (KwaZulu-Natal) may be assumed. *Schusteria ugraseni* was known to occur from Mazeppa Bay (Eastern Cape) to Durban (KwaZulu-Natal) and now a distribution from East London to Durban is confirmed. Procheş and Marshall (2002, p 1207) also reported the occurrence of *Schusteria* sp. 2 at St Lucia, which most likely refers to *Selenoribates divergens*, which we found to be present in this area. Unfortunately, the material mentioned by those authors is no longer available, and hence this statement remains an assumption. Procheş and Marshall (2002, p 1207) also reported the occurrence of *Schusteria* sp. 2 at St Lucia, which most likely refers to *Selenoribates divergens*, which we found to be present in this area. Unfortunately, the material mentioned by those authors is no longer available, and hence this statement remains an assumption. Procheş and Marshall (2002, p 1207) also reported the occurrence of *Schusteria* sp. 2 at St Lucia, which most likely refers to *Selenoribates divergens*, which we found to be present in this area. Unfortunately, the material mentioned by those authors is no longer available, and hence this statement remains an assumption.
### Table 1: Climate data (obtained from www.SeaTemperature.org and the South African Weather Service) and confirmed occurrences of intertidal oribatid mite taxa for 23 locations along the South African coast. Asterisks (*) refer to reports from earlier literature (Procheş and Marshall 2002); the location between rules represents the distributional border between the cold-adapted podacarid and the warm-adapted fortuyniid and selenoribatids

| Location                | Coordinates            | Sea surface temperature (°C) | Air temperature (°C) | pH | Humidity (%) | Taxa found         |
|-------------------------|------------------------|-----------------------------|----------------------|----|--------------|-------------------|
|                         | Min. | Max. | Mean | Min. | Max. | Mean | Halozetes | Fortuynia | Schusteria | Selenoribatids |
| Lambert's Bay           | 14.5 | 17.5 | 16.0 | –    | –    | –    | 99 | 0 | 0 | 0 |
| Langebaan               | 15.1 | 18.4 | 16.8 | 8.5  | 23.2 | 14.3 | 7.8 | 73 | 0 | 0 |
| Camps Bay               | 15.4 | 18.5 | 17.0 | 14.2 | 22.0 | 16.3 | 7.7 | 82 | 0 | 0 |
| Kommetjie               | 16.4 | 19.3 | 17.9 | –    | –    | –    | –   | 1* | 0 | 0 |
| Hermanus                | 16.8 | 19.3 | 18.1 | 13.8 | 21.1 | 16.1 | 8.1 | 59 | 1* | 0 |
| De Hoop Nature Reserve | 16.4 | 19.2 | 17.8 | 10.5 | 23.8 | 15.4 | 8.3 | 46 | 1 | 0 |
| Stilbaai                | 16.8 | 19.6 | 18.2 | –    | –    | –    | 8.1 | 68 | 0 | 0 |
| Mossel Bay              | 17.5 | 20.5 | 19.0 | 14.0 | 21.6 | 16.7 | 8.2 | 65 | 0 | 0 |
| Hermanus                | 16.5 | 19.8 | 18.1 | –    | –    | –    | 8.3 | 65 | 0 | 0 |
| Victoria Bay            | 16.5 | 19.8 | 18.1 | 11.7 | 21.7 | 15.1 | 8.1 | 80 | 1 | 0 |
| Plettenberg Bay         | 16.5 | 20.4 | 18.4 | 13.9 | 21.6 | 16.7 | 8.2 | 88 | 1 | 0 |
| Port Alfred             | 19.7 | 21.6 | 21.1 | –    | –    | –    | 8.2 | 63 | 1* | 0 |
| East London             | 21.3 | 24.5 | 22.7 | 14.7 | 24.1 | 19.4 | 8.1 | 70 | 0 | 1 |
| Mazeppa Bay             | 22.0 | 24.8 | 23.4 | 15.3 | 24.9 | 19.5 | –   | 0 | 0 | 1* |
| Port St Johns           | 22.3 | 25.2 | 23.8 | –    | –    | –    | 8.2 | 96 | 0 | 1 |
| Port Edward             | 22.3 | 25.3 | 23.8 | 17.1 | 23.7 | 20.1 | 8.2 | 90 | 0 | 1 |
| Port Shepstone          | 22.5 | 25.4 | 23.9 | –    | –    | –    | 8.5 | 90 | 0 | 0 |
| Ummombaas               | 22.5 | 25.4 | 23.9 | –    | –    | –    | 8.1 | 90 | 0 | 1 |
| Amanzimtoti            | 22.4 | 25.2 | 23.8 | –    | –    | –    | 8.2 | 90 | 0 | 0 |
| Salt Rock               | 22.4 | 25.3 | 23.8 | –    | –    | –    | 8.4 | 92 | 0 | 1 |
| Durban (Umdloti)        | 22.4 | 25.3 | 23.8 | 16.5 | 25.1 | 20.0 | 8.3 | 90 | 0 | 1 |
| St Lucia                | 23.1 | 25.7 | 24.4 | 17.4 | 27.8 | 21.3 | 8.3 | 85 | 0 | 0 |

* Asterisks (*) refer to reports from earlier literature (Procheş and Marshall 2002).
(2002) indicated a distribution of *H. capensis* from Kommetjie (Western Cape) to Port Alfred (Eastern Cape), whereas our data demonstrate that its eastern distribution reaches beyond Port Alfred, to Kayser’s Beach near East London. All these species are clearly typical components of the intertidal South African fauna, and despite some gaps remaining at certain locations we can assume continuous distributions of each species along the coastline.

**Biogeographic patterns**

The terrestrial fauna and flora of South Africa’s coastline are subject to a very diverse climate consisting of several different regions (e.g. Köppen and Geiger 1936) (see Figure 2). Mapping these regions onto the distributions of intertidal oribatid mites reveals only partly conclusive patterns. The occurrences of the fortuyniid and selenoribatids are mostly confined to the humid subtropical climate region of South Africa’s east coast, with only *S. ugraseni* also occurring in the oceanic climate near East London. The podacarid can be found in oceanic and hot semi-arid climates of the south coast as well as in the Mediterranean climate stretching from Cape Agulhas to Cape Point, which indicates that terrestrial climates may not be the primary factor shaping the biogeography of at least the podacarid. Comparing the distributions with the proposed marine biogeographic ecoregions (i.e. the Southern Benguela, Agulhas, Natal and Delagoa ecoregions; Spalding et al. 2007; Sink et al. 2012) provides a more conclusive picture. The fortuyniid and selenoribatids are clearly distributed in the Natal Ecoregion, and the podacarid in the Agulhas Ecoregion, whereas the podacarid *H. capensis* population found at Kommetjie (Prochêq and Marshall 2002; Coetzee and Marshall 2003) is in the Southern Benguela Ecoregion. Kommetjie lies only 25 km north of Cape Point, which has been suggested to be the break between the Benguela and the Agulhas ecoregions (e.g. Stephenson and Stephenson 1972; Emanuel et al. 1992; Spalding et al. 2007; Sink et al. 2012); therefore, this occurrence may still be interpreted as being within the Agulhas Ecoregion.

Despite their relatively recent marine connections, intertidal mites were suggested to show typical geographical
distributions conforming with those of southern African marine taxa in general (Procheş and Marshall 2002), and this is supported by the present findings. However, many of the marine taxa are not narrowly defined to a certain ecoregion but show considerable transition or zones of overlap. For seaweeds, two transition regions have been identified: a western overlap between cool-temperate west coast flora and warm-temperate south coast flora in the area of Cape Agulhas (Bolton 1986; Anderson et al. 2009), and an eastern overlap between the warm-temperate south coast and subtropical east coast flora in the region of Hluleka, Transkei (Eastern Cape Province) (Bolton and Stegenga 1987). For coastal fishes, the warm-temperate/subtropical boundary was suggested to occupy a vast transition zone stretching about 100 km north and south of Port St Johns (Turpie et al. 2000), and similar transition zones in the vicinity of Port St Johns and East London were postulated for diverse intertidal biota (Stephenson and Stephenson 1972; Emanuel et al. 1992). Such a transition zone has not been detected for ameronothroid mites; there is a gap of only ~20 km, from Kayser's Beach to Winterstrand, between supposedly cold-adapted and warm-adapted taxa, and this gap coincides with the suggested border between the warm-temperate Agulhas and the subtropical Natal ecoregions (Emanuel et al. 1992; Bustamante and Branch 1996; Sink et al. 2012) near East London. Although we do not have sampling data from within this small gap, and thus do not know the exact distributional borders, we assume that there are no overlapping areas in the form of the considerable transition zones that have been shown in many other groups (e.g. Bolton and Stegenga 1987; Turpie et al. 2000).

The fortuyniid and selenoribatids clearly occupy the Natal Ecoregion, and though this study has St Lucia as its northeasternmost site the distributions of these species are known to stretch far beyond the borders of this area as occurrences have been reported from the coasts of

Figure 2: Distribution of intertidal oribatid mite families shown on a map highlighting terrestrial climate regions of South African shorelines (Köppen and Geiger 1936) and coastal ecoregions (Spalding et al. 2007; Sink et al. 2012); the key refers only to terrestrial regions. F = Fortuyniidae; P = Podacaridae; S = Selenoribatidae
Mozambique and Kenya (Luxton 1986; Marshall and Pugh 2000, 2002). Bolton et al. (2004) demonstrated a changeover from a tropical Indian Ocean seaweed flora to a temperate South African flora in the vicinity of St Lucia. Those authors further stated that intertidal mite patterns closely mirror the available seaweed data and therefore they hypothesised a

![Figure 3: Mean annual (a) sea surface and (b) air temperatures of sample locations, from west to east (left to right); numbers refer to locations indicated on the outline of South Africa’s coastline (middle panel). Grey shaded areas indicate the distributional ranges of the respective species based on their family designations. NP = national park; NR = nature reserve](image-url)
similar changeover to a tropical intertidal mite fauna in the St Lucia region. Based on the present data, we cannot confirm this hypothesis, but a sudden change of species composition in this region is indeed observable. *Fortuynia elamellata micromorpha* and *Schusteria ugraseni* are common from Port St Johns to Durban, but at St Lucia only *Selenoribates divergens* was found, though different *Fortuynia* and *Schusteria* species have been reported farther northeast, in Mozambique (Marshall and Pugh 2000, 2002). Accordingly, *F. elamellata micromorpha* and *S. ugraseni* may be endemic to the subtropical Natal Ecoregion, and the above-mentioned changeover to more-tropical taxa representing the Delagoa Ecoregion at St Lucia may be real. However, sampling efforts on the tropical east coast of Africa have been largely incomplete and much more research on the mite fauna in this area is necessary to confirm such a biogeographic pattern.

On the west coast, intertidal oribatid mites could not be detected in the cool-temperate Southern Benguela Ecoregion, except for the above-mentioned occurrence of the podacarid *H. capensis* in the southern border region at Kommetjie (Pročeh and Marshall 2002; Coetzee and Marshall 2003). Apparently, environmental conditions within the Southern Benguela Ecoregion are unsuitable for any intertidal oribatid mite. However, samples in this region were only taken from Cape Point to Lambert’s Bay (Pročeh and Marshall 2002; present study), which leaves more than 400 km of shoreline north of this area uncharted in terms of intertidal mite fauna. Therefore, it is possible that *H. capensis* or other intertidal oribatid mite taxa are present there but have not yet been detected.

Nevertheless, most of the South African coastline has been thoroughly studied and all of the found and widely distributed species represent endemic species for this area, except for *S. divergens*. The South African marine invertebrate fauna is known to show a high level of endemism, which is attributed to the isolation of southern Africa and the prevailing ocean current system precluding dispersal from the south and west (Pročeh and Marshall 2002). Intertidal oribatid mites neither have pelagic larvae nor show any kind of active swimming behaviour, but their main mode of dispersal is reported to be via ocean currents (e.g. Schatz 1991; Pfingstl 2013). The warm Agulhas Current has been demonstrated to be a major factor influencing the distribution of tropical and subtropical estuarine and marine fishes along the east coast and the dispersal of these species in a southerly direction (van der Elst 1981; Turpie et al. 2000). The distributions of the fortuynid and selenoribatids coincide with the warm and rapid Agulhas Current flowing southward along the subtropical east coast (Figure 4), and, assuming dispersal via this current, it is likely that their ranges are also derived from a strong incursion of Indo-Pacific faunal elements (Pfingstl 2016) and thus show dispersal only in a southward direction.

*Halozetes capensis* is clearly derived from subpolar ancestors as all other members of this genus are widely distributed on the peri-Antarctic Islands, the Antarctic Peninsula and southern New Zealand (Coetzee and Marshall 2003). Whether this species is a relic of Gondwanaland or of a recent glacial period, or the result of a long-distance dispersal event, cannot be determined without appropriate molecular genetic data. The present distribution of *H. capensis* is mainly restricted to the area of the Agulhas Bank, where the Agulhas Current moves away from the coast and some warm eddies (Agulhas rings) continue westward and mix with the cooler Benguela waters near Cape Point (e.g. Morris et al. 2017); therefore, it can be assumed that dispersal of this podacarid species occurs mainly in a westward direction, although the eddies and gyres might also result in occasional eastward dispersal events.

**Influence of ecological factors**

South Africa has more than 878 described seaweed species (Mucina et al. 2006). The diversity of seaweeds is twice as high on the south and east coasts compared with on the west coast. Intertidal oribatid mites use intertidal algae as a substrate and food source (Pfingstl 2017); thus, it is not surprising that biogeographic patterns of intertidal mites were suggested to closely mirror seaweed distributions (Bolton et al. 2004). Nonetheless, intertidal oribatid mite distributions are clearly defined in accordance with South African marine biogeographic regions, whereas seaweed distributions have been demonstrated to show large transitional zones with a gradual change from warm-water to cold-water species (Farrell et al. 1993; Bolton et al. 2004). In the present study, we found the mite species in the midlittoral *Gelidium* or the upper eulittoral *Bostrychia* and there are several species of these algae (*Gelidium*: 11 species; *Bostrychia*: 7 species) on South Africa’s coast, most with overlapping distributions and only a few with distinct distributions. Marine-associated oribatid mites have been reported to be generalised feeders, with various degrees of preferences (e.g. Pfingstl 2017). Consequently, they are relatively flexible when choosing their food, which means their occurrence most likely does not depend on the presence of a specific species or type of seaweed.

**Climatic factors**

Geographical distributions of southern African marine faunas are mostly governed by the seawater temperature along the coast, which in turn is affected by the two large current systems present in this region (e.g. van der Elst 1981; Field and Griffiths 1991). On the seashore, analysis of temperature effects is made especially difficult by the presence of numerous factors, such as daily tidal rhythm with alternating emergence and submergence, and thus it is difficult to determine the relative importance of sea and air temperatures (Southward 1958). As rocky shore habitats are exposed to direct solar radiation, air temperature is a poor predictor during tidal emersion. The mites are very small and it is unknown whether they show specific behavioural thermoregulation, so it is difficult to assess precisely what temperatures they experience during low tide. However, the factors of habitat heterogeneity, solar radiation, and behavioural thermoregulation become irrelevant once the mites become submersed in seawater again. Accordingly, air temperature may not provide conclusive insight into the relationship between climate and the distributions of these mites. The marine-associated Ameronothroidea, however, have been suggested to represent a model case of biogeography because their distributions are linked to the world’s climatic regions (e.g. Luxton 1967).
However, the importance of oceanographic climates in shaping these patterns has never been seriously considered or studied, although it was argued that ocean currents may well play a role (Pfingstl and Schuster 2014; Pfingstl et al. 2019). When comparing the distributions of South African intertidal oribatid mites with the terrestrial and oceanographic climates, it becomes apparent that occurrences correspond exactly with marine biogeographic ecoregions and thus with ocean currents and their respective temperatures. The boundary between the cold-adapted podacarid and the warm-adapted fortuyniid and selenoribatids lies in the area of East London. Exactly in this area, the warm Agulhas Current moves well offshore, following the edge of the Agulhas Bank (Gründlingh 1983), which results in a significant drop of water temperature, whereas the shift in air temperature is only gradual. Moreover, annual air temperatures in the distributional ranges of the podacarid and the fortuyniid/selenoribatids show overlap whereas annual water temperatures in the respective ranges are clearly distinct. These findings indicate that oceanographic climate is the most important factor controlling the distributions of these taxa.

Dispersal of a species is stopped by the inability of the individuals to survive excessive cold or heat and by critical...
temperatures necessary for reproduction and completion of life cycles (Hutchins 1947). Annual seawater temperature means along the South African coast range from 14 to 26 °C, and air temperature means from 8 to 28 °C during the year—temperatures that are most likely non-lethal for any of the given mite species. Thus, temperature stress for reproduction and development, which exhibits a narrower range within the survival limits (Hutchins 1947), is presumably the governing factor. However, detailed temperature-tolerance experiments are necessary to assess the exact limits of survival, reproduction and development. Moreover, Southward (1958) has already argued that intertidal animals of rocky shores show an upward shift of the range of temperatures experienced compared with the temperature of tide pools or air on the shore. Accordingly, it can be assumed that the animals are subject to a wider range of temperatures than are observed in local climate data.

Global climate change

The South African climate has changed in recent decades, with the eastern region (KwaZulu-Natal) and western region (Western Cape) having experienced significant warming trends over the past 50 years (Warburton et al. 2005). Spatially, significant trends in mean annual maximum temperature were mostly recorded close to the coast (Kruger and Shongwe 2004). As a further consequence of global warming, the sea level is rising at a rate of 3.7 mm year⁻¹ (see Kirwan et al. 2016 for global rates) and an increase in the frequency and intensity of winter storms along the coast of South Africa has been predicted (Theron and Rossouw 2008). Increasing sea level is not expected to have major consequences for most coastal species, as they can simply move higher up the shore, but many shores on the South African east coast consist of rock platforms which are bounded by sandy habitats above, and here rising sea levels may result in the loss of habitat (Griffiths et al. 2010). Apart from this potential threat for local populations of intertidal oribatid mites, global-warming-induced changes in sea surface temperatures will certainly change their geographic ranges. The warm-adapted fortuniiid and selenoribatids can be expected to expand their ranges southward, while the cold-adapted podacarid might be reduced to a few southwestern coastal areas in the next few decades.

In conclusion, the present study represents important baseline data for future studies that might give more detailed insights into the effects of climate change on coastal organisms in general.

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