

SHORT COMMUNICATION

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Large fluctuations but constant mean temperatures allow corals to persist in intertidal rock pools on the east coast of South Africa

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Abstract

Intertidal corals have been under-studied yet they provide scope for understanding adaptation and acclimatisation of corals to marginal conditions. Corals in intertidal rock pools along the east coast of South Africa withstand large temperature fluctuations, and marginal conditions for survival and growth. Four sites along the KwaZulu-Natal (KZN) coastline were sampled to determine latitudinal differences in coral communities, from 27°S to 31°S. Water temperature of rock pools at each site was monitored to see if temperature determined coral diversity in intertidal pools. Sixteen coral species were present in rock pools overall. Each of three sites in northern and central KZN hosted 12 coral taxa whereas only six taxa occurred at the most southern site. *Anomastrea irregularis* was the most abundant species at all sites, followed by *Pocillopora verrucosa* and *P. damicornis*. Unexpectedly, rock pool temperatures did not show a trend with latitude and thus cannot explain this decline in coral diversity. Temperatures in isolated rock pools showed large summer day time fluctuations of more than 10 °C at spring tide. However, temperatures drop substantially at high tide, lowering the mean rock pool temperature and possibly allowing these coral communities to persist in the marginal conditions of rock pools in South Africa.

Keywords: Intertidal, Temperature, Rock pools, Hard coral, *Pocillopora verrucosa*, *Anomastrea irregularis*

Background

'Marginal' environments are characterised by sub-optimal, fluctuating conditions [1]. For corals, this definition can be refined to refer to habitats that occur near or beyond the limits of natural coral distribution, based on physical factors including light, temperature and salinity [2]. The intertidal zone is a highly dynamic, benthic environment, imposing a variety of physical stresses on biota, including possible periodic aerial exposure, fluctuations in temperature and salinity, high solar radiation and strong wave action and sedimentation, over short periods [3, 4]. Intertidal environments are thus marginal coral habitats and corals occurring there must tolerate harsh environmental conditions [3, 5]. Nonetheless, rich coral communities occur in intertidal reef habitats despite

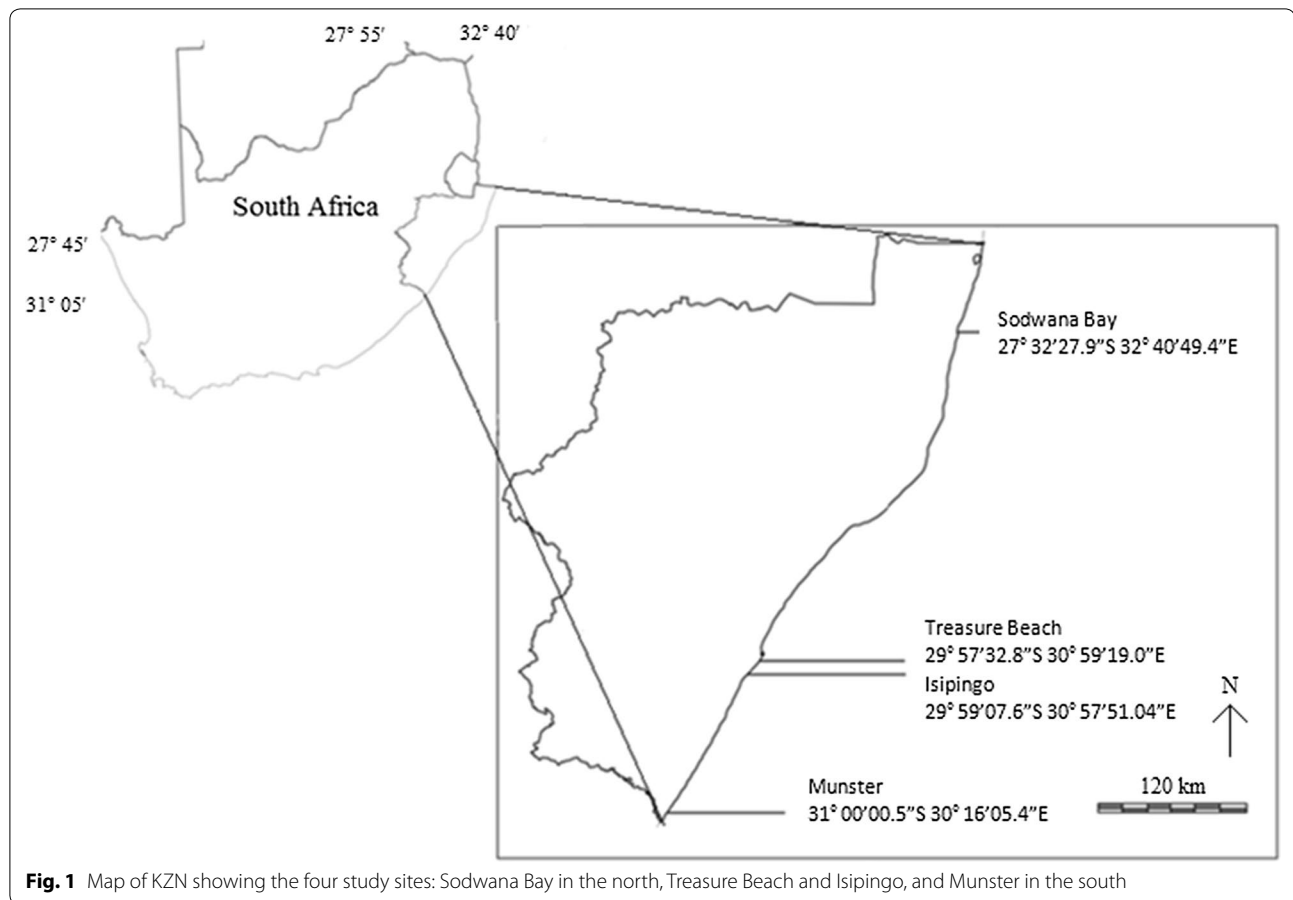
the harsh conditions [4] and may be used as models to understand resilience, including to climate change, in coral assemblages [4, 6]. Reef environments considered marginal today may become important under future climate conditions according to models [7], although intertidal habitats were not specifically included in the model.

Intertidal rocky shores of KwaZulu-Natal (henceforth KZN), on the east coast of South Africa (Fig. 1) are inhabited by a variety of scleractinian coral species. Although corals in the intertidal zone have been documented at several locations [e.g. 7–9], few studies have surveyed intertidal zones at high latitudes such as this. Little research has been conducted on the diversity or distributions of intertidal corals in the region, but corals have been observed as far south as Munster, at latitude 31°04'S. Coral abundance was generally low in KZN rock pools, with some species represented by only one or two colonies, exceptions being *Anomastrea irregularis*, *Pocillopora verrucosa* and *P. damicornis* [10]. The only other published literature on these coral populations in South

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Africa is the genetic connectivity of *Acropora tenuis* along KZN [11], and the sexual reproduction of *Pocillopora damicornis* in rock pools [12].

Temperature is considered a major constraint on coral distribution, with corals restricted to relatively narrow thermal ranges. Coastal summer sea surface temperatures (SSTs) in northern KZN, measured by underwater temperature recorders, ranged from 27 to 29 °C between 1993 and 2006 [13], while mean summer temperatures on the south coast ranged from 20.5 to 22.4 °C [14]. Coastal winter temperatures vary from 22.2 °C on the north coast to 19.4 °C on the south coast [14]. A considerable temperature gradient is thus evident along the coast, particularly in summer.

The highest diversity of scleractinian corals is observed at low latitudes, where sustained warming of sea surface temperatures is often the main cause of coral mortality on subtidal reefs [15–17]. Low temperatures for sustained periods can however also affect coral survival [18]. This can be particularly significant for corals in temperate regions. For example, an extreme weather event resulted in a significant loss of coral diversity and abundance in the Hervey Bay, Australia [19]. Similar extreme weather

and climatic events have also resulted in a loss of coral diversity or abundance [19], but this is usually over a prolonged period.

Tolerance to thermal stress is imperative for corals [20], and those taxa already found in marginal habitats for coral growth and survival may be less susceptible to future changes in climate and local environmental conditions [1, 18]. Temperature patterns, sea surface temperature regimes and the response of corals are extensively studied globally, yet with focus on subtidal reef habitats [e.g. 5, 9, 16]. The occurrence and distribution of intertidal scleractinian coral species is however poorly documented particularly at high latitudes, let alone the local temperature patterns within these habitats. This information should provide a better understanding of the tolerance and resilience of scleractinian corals to thermal stress and help to predict the state of future coral assemblages in an era of global climate change.

Based on local sea surface temperature data collected from the east coast of South Africa, it is predicted that similar seasonal and latitudinal patterns would be expected in the intertidal zone; however no in situ

temperature data has been recorded from rocky shores on the South African coastline to date.

We therefore surveyed the hard corals in rock pools along length of the KZN coastline to determine the diversity of species in pools at each site. We measured temperature variation in pools at each site for a year to determine whether differences in temperature could explain changes in coral diversity among sites. We hypothesised that lower temperatures would restrict the southerly distribution of corals in rock pools.

Methods

Study site

This study was conducted on the east coast of South Africa, in the KwaZulu-Natal (KZN) province (Fig. 1). The South African coastline experiences a semi-diurnal tidal cycle with a range varying from 1.5 to 2.23 m. Intertidal rocky shores are thus exposed for approximately 4 h twice a day during spring tides. Inshore habitats in KZN are divided between two bioregions, the Delagoa region in the north and the Natal bioregion in the rest of the province, with the break at Cape Vidal, south of Sodwana Bay [21], although this categorisation may not apply to all faunal groups [14]. Four sites were chosen along the length of KZN (Fig. 1). The northern-most and only site within the Delagoa bioregion (Fig. 1) was Jesser point at Sodwana Bay (27°3'27.9"S 32°40'49.4"E). Two sites, Treasure Beach and Isipingo, in the centre of the province and a southern site at Munster (31°00'00.5"S 30°16'05.4"E) all occur in the Natal bioregion. Sodwana Bay is classified as a wave-cut rocky platform while the other sites are classified as exposed rocky headlands [22]. Wave cut rocky platforms are horizontally-orientated rock surfaces, created by the erosion by waves along a relatively high energy coastline, while exposed rocky headlands are more vertically-oriented rock surfaces, an extension from the land [22]. Despite these differences, the rock pools at each of our study sites occurred at near-horizontal surfaces between the high- and low-tide marks.

Sampling

The number of rock pools sampled varied per site, as the aim was to survey the coral community at each site as thoroughly as possible and all rock pools within a demarcated site were surveyed. The sampling area at each site was demarcated to approximately 150 m in length and 30 m in width. At least one colony of every coral species present was photographed using a Nikon underwater camera or a GoPro Hero3®. Corals were identified to species level or to the highest resolution possible.

At three of the four sites, one rock pool was selected for water temperature measurement. Rock pools of similar size and depth were chosen, but it was impossible to

avoid some variation among sites, particularly in the case of Munster where pools were smaller than at the other sites (Table 1). Nevertheless this is suitable to determine a general temperature pattern in isolated rock pools at different latitudinal positions, which is not documented along the east coast of South Africa.

Temperature data were collected using small data loggers, (iButtons Maxim®, San Jose, CA, US), cross calibrated in the laboratory with an accuracy of ± 0.2 °C. Individual iButtons were sealed in a waterproof silicon casing and attached to the rocky substrate, out of sight of casual visitors, using waterproof epoxy putty, Aquamend™. Two iButtons were attached at depths of 20–30 cm in each pool. Physical descriptions of each pool were measured (Table 2), and iButtons were never exposed to the air at spring low tide. Loggers were set to record temperatures every 30 min and were replaced every 4–6 weeks, for 1 year. Some iButtons were however lost in the field, and data were not retrieved for these periods, resulting in some missing seasonal data. In particular, no data were collected in summer at Sodwana Bay. Daily temperature ranges were plotted for each season at each site.

Data were analysed using IBM SPSS vol. 21 and Graphpad Prism vol. 5. The temperature data were not normally distributed despite log and square root transformations, thus a non-parametric one-way repeated measures Analysis of Variance (ANOVA) was used to compare mean temperature among sites. A Friedman test was used to assess differences in seasonal temperature ranges among sites in autumn and winter. Where significant differences were found a Wilcoxon signed-rank test was used to compare significant differences for all site combinations. A Wilcoxon signed-rank test was also used to compare summer temperature data between Munster and Isipingo, the only two sites where summer temperature is available.

Results

Eight scleractinian coral families occurred in the intertidal zone along the KZN coast with a total of 16 species (Table 2). Merulinidae have the highest representation

Table 1 Physical description of each rock pool used for temperature data collection

	Munster	Isipingo	Treasure Beach	Sodwana Bay
Length (m)	1.50	1.70	1.60	1.30
Width (m)	0.90	0.90	1.00	1.00
Surface area (m ²)	1.40	1.53	1.60	1.30
Depth (m)	0.20	0.50	0.40	0.80
Estimated volume (m ³)	0.37	0.77	0.64	1.04

Temperature data were collected from 1 rock pool per site

Table 2 Biodiversity of scleractinian corals in the intertidal rock pools of KwaZulu-Natal, at four sites

Family	Genus	Species	Sodwana Bay	Treasure Beach	Isipingo	Munster
Pocilloporidae	<i>Pocillopora</i>	<i>verrucosa</i>	*	*	*	*
		<i>damicornis</i>	*	*	*	
	<i>Stylophora</i>	<i>pistillata</i>		*		*
Acroporidae	<i>Acropora</i>	(a)	*	*	*	
		(b)		*	*	
Siderastreidae	<i>Anomastrea</i>	<i>irregularis</i>	*	*	*	*
Agariciidae	<i>Pavona</i>	<i>venosa</i>	*	*	*	
Mussidae	<i>Acanthastrea</i>	<i>echinata</i>	*	*	*	*
		<i>Blastomussa</i>			*	
	Unidentified		*	*		
Merulinidae	<i>Hydnophora</i>	<i>exesa</i>	*	*	*	
		<i>Favia</i>			*	
		<i>speciosa</i>	*			*
	<i>Favites</i>	<i>pentagona</i>	*	*	*	*
	<i>Goniastrea</i>	(d)	*			
Poritidae	<i>Porites</i>	(e)	*	*	*	

Species is unknown for those marked (a–e)

* Represents at least one observation of that group

of coral genera and species, followed by Pocilloporidae and Mussidae. High coral diversity occurs in the northern and central parts of the province, with Isipingo and Treasure Beach hosting an equal number of families and genera to Sodwana Bay (Table 2). A lower coral diversity is then suddenly observed at Munster. However, six coral species from four families are still present there (Table 2).

Temperature fluctuations at Munster and Isipingo are larger in summer than in winter (Figs. 2, 3). Maximum temperature fluctuations occur at spring tides when isolation of pools from the sea is longest, and when pools are isolated and exposed to the sun accentuating temperature differences between day and night. During summer, temperatures at Munster and Isipingo may experience a 10 °C

change over one tidal cycle (Fig. 2). The lowest and highest recorded temperatures were 19.5 and 32.5 °C respectively (Table 3). Conversely, winter temperatures change by only 2–4.5 °C throughout one tidal cycle (Fig. 2). Temperature variation differs significantly between seasons, taking into account all sites [$\chi^2(2) = 8.300$, $P = 0.021$]. Post hoc tests showed that summer (at Munster and Isipingo) had the highest temperature range ($Z = -1.0832993$, $P = 0.008$), with temperature variation in autumn significantly higher than winter ($Z = -0.0542993$, $P = 0.030$).

There was also a significant difference in temperature between sites during autumn and winter [$\chi^2(2) = 6.211$, $P = 0.021$], with Munster experiencing larger temperature fluctuations than at Isipingo

Table 3 The seasonal mean, minimum, maximum and range of rock pool temperatures at each site along the South African coast

Site	Season	Water temperature (°C)				
		Mean	SD	Min	Max	Range
Sodwana Bay	Autumn	23.06	0.97	16.50	26.50	10.00
	Winter	21.72	1.07	17.50	25.00	7.50
Isipingo	Summer	24.68	1.88	21.50	32.00	10.50
	Autumn	22.15	0.99	20.50	26.50	6.00
	Winter	21.16	2.20	17.50	24.00	6.50
	Summer	23.40	1.98	19.50	32.50	13.00
Munster	Autumn	21.91	1.48	17.00	30.00	13.00
	Winter	22.02	0.74	18.50	26.00	7.50

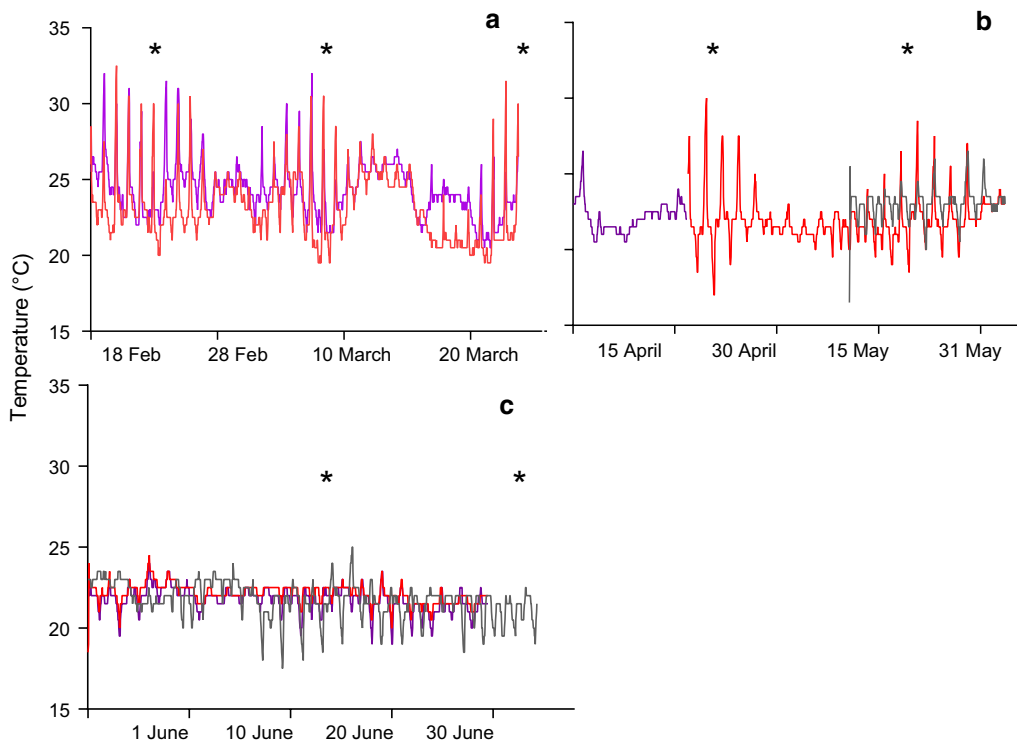


Fig. 2 Daily temperature range in the intertidal rock pools of KwaZulu-Natal in 2013, during summer (a), autumn (b) and winter (c) at Munster (red), Isipingo (purple) and Sodwana Bay (gray). Temperatures were logged every 30 min. Not all sites are represented. Stars represent spring tides

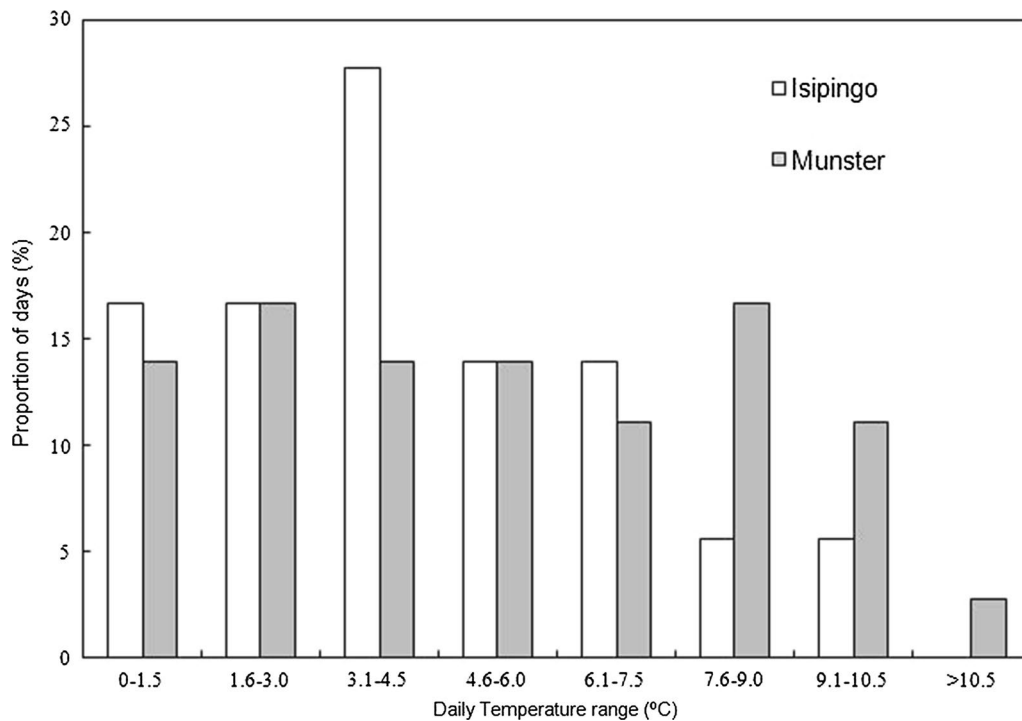


Fig. 3 The percentage occurrence of daily temperature ranges during summer at Munster and Isipingo

($Z = -1.343$, $P = 0.005$). Munster experiences the largest change in temperature in April, with a minimum and maximum temperature of 17 and 30 °C respectively (Fig. 2, Table 3). In winter, temperatures range from 17.5 to 26 °C across all sites (Table 3). Maximum temperatures at Munster are also higher than all other sites in autumn and winter (Table 3).

Mean temperature differed significantly among sites only during autumn and winter [autumn: $\chi^2(2) = 6.118$, $P = 0.027$; winter: $H = \chi^2(2) = 2.699$, $P = 0.0$]. However, differences were often less than 1 °C among all the sites. Mean summer temperatures at Munster and Isipingo were 23.40 and 24.68 °C respectively (Table 3). Mean winter temperatures at each site were 22.02 °C at Munster, 21.16 °C at Isipingo and 21.72 °C at Sodwana Bay (Table 3).

Discussion

A total of sixteen coral species occurred in pools along the coast. Rock pools in central KZN host as many coral species as the rock pools in Sodwana Bay, a more tropical environment (Table 2). Twelve species from seven families were present in pools at each of these locations, however coral diversity declines sharply at Munster with only six hard coral species present from four families (Table 2). These families included Pocilloporidae, Siderastreidae, Mussidae and Merulinidae. *Pocillopora* was the most abundant genus along the entire coastline, confirming previous observations [10] and attesting to the persistence of the population. Additionally, this study found very high abundances of *A. irregularis* at all sites, with up to 400 individuals at Isipingo (K. Smit, unpublished data).

Species occurring at the southernmost site in this study have also been surveyed at other high latitude reefs, despite the lack of surveys in similar intertidal habitats. The genera *Pocillopora* and *Stylophora* are common at high latitudes [19, 20, 23]. Corals of these genera are widespread, hardy and abundant in most reef habitats [24], often being referred to as ‘weedy’ or ‘tramp’ species. However, they are not regarded as being particularly resilient to thermal stress [25, 26]. *Anomastrea irregularis*, to our knowledge, has only been previously reported at a high latitude reef in the Arabian Gulf [23], but since its distribution is limited to the Western Indian Ocean region and the Gulf [24], there are limited possible locations for its occurrence. *Favia speciosa*, *Favites pentagona*, and *Acanthastrea echinata* are all common species in a wide range of habitats and have been recorded at multiple high latitude reefs in Japan, Australia, the Arabian and Persian Gulf [19, 20, 23, 27].

Faviids are more tolerant to marginal high latitude habitats and are generally resistant to stress [28, 29]. In contrast, *Acropora* or *Porites* tend to dominate at lower

latitudes. Furthermore, Mizerek et al. [30] suggest that tabular, encrusting and massive species, and those with similar traits, are more likely to persist “beyond reef” habitats or latitudes. Aside from the Pocilloporidae, all other taxa observed in this study exhibit massive or encrusting growth forms. Thus all the species observed at the southern limit of our study are either hardy, common corals or are known to be opportunistic in a variety of reef habitats. Species assemblages of several exposed intertidal habitats in South Africa differ between the tropical Delagoa bioregion, in which Sodwana bay falls and the subtropical Natal bioregion where the other three sites are situated [21]. These include the fauna of exposed intertidal habitats [21] fish [31] and subtidal reef corals [13, 32] which all decline southwards along the KZN coast. We therefore expected a similar decline in coral species diversity and colony abundance in the intertidal zone. However, intertidal coral diversity is maintained into the central parts of KZN, across the boundary of the two bioregions.

The number of hard coral species observed in pools at the central sites in this study was comparable to the number on Aliwal Shoal, a nearby subtidal reef [33], further suggesting that conditions in intertidal pools at these sites were not the major constraint on species diversity. Although far more species have been observed in intertidal habitats of reef flats [4], the isolated pools of subtropical intertidal shores in this study provide a far more restricted habitat and a less species rich assemblage was expected.

In part, the high diversity of species observed in the central parts of the province may be due to the similarity of water temperatures in rock pools along the coast. Although statistically significant the mean temperature difference among sites, was less than 1 °C during autumn and winter and during summer at Munster and Isipingo. This contrasts with the sub-littoral sea surface temperature, which declines southward along the coast [14]. There were nevertheless considerable differences in temperature ranges among sites, which may be attributed to the properties of individual pools. Although no data were collected in summer for Sodwana Bay, the absence of significant temperature differences between this and other sites in the remaining seasons implies that the absence of a gradient would extend to Sodwana Bay in summer.

Rock pool temperatures at Munster, the southernmost site, remain high and experienced some of the largest temperature fluctuations (Fig. 2). The pool at this site had the lowest volume of all the pools in which temperature was measured (Table 1), making it susceptible to large temperature variations, especially during summer days. If the pools at this site were generally smaller than at other sites, the increased temperature range could

partially explain the decline in species diversity at this site and the occurrence only of hardy or weedy coral species. Larger pools with a larger volume of water have a higher heat capacity, thus it requires more energy to heat the water temperature. Thus, the lower heat capacity of smaller and/or shallower rock pools creates more heating and higher temperatures during exposure at low tide, and also greater and faster heat loss as the tide comes in. Further cooling as the tide comes in lowers rock pool mean temperatures, likely allowing these corals to acclimatise to such temperature cycles. Corals in these pools did not suffer aerial exposure at low tide, as has been observed elsewhere [4], possibly facilitating their resilience in these pools.

The water temperature of intertidal rock pools in KZN undergoes large diel fluctuations over short periods (Figs. 2, 3). In summer and during daytime spring low tides, when pools are isolated and exposed to the sun for roughly 5 h, temperatures can fluctuate more than ten degrees over as little as 2 h. Large temperature fluctuations are common for corals inhabiting shallow-water environments, however we did not find studies that have reported daily temperature ranges as high as this study [e.g. 8, 34, 35]. Summer diel temperature fluctuations of 5–6 and 8.2 °C occurred in reef flats near Java and in the Gulf of Oman respectively [34, 35], while temperatures in isolated pools of different sizes in American Samoa fluctuated by no more than 6.9 °C over the tidal cycle [8]. Java and Samoa are more tropical than those of this study yet maximum rock pool temperatures in this study are comparable [8, 36]. Thus it appears that rock pools at higher latitudes in temperate environments tend to cool down to lower temperatures, especially at night, therefore increasing the daily range, as shown by this study.

Although, sustained low mean temperatures, specifically less than 18 °C, can also have a detrimental effect on the survival of hard corals, particularly in subtropical or temperate climates [18, 19]. Results from this study showed that temperature fluctuations in isolated rock pools would be considered extreme for subtidal coral reefs. Large colonies of *P. verrucosa* were observed throughout the study, with an average length of 15 cm, some reaching up to 28 cm in length (K. Smit, personal observation, unpublished data). Large colonies of *A. irregularis* were also observed, among other individuals of massive coral taxa. Thus temperature patterns over the past few years were unlikely to have affected the mortality of rock pool corals.

Extreme weather and sea temperatures [18, 19, 37] may cause the mortality of local coral populations. Along the coastline of KZN, temperatures measured in rock pools were neither variable, high nor low enough to prevent corals persisting. Although this was a short term study

and may not encompass the full range of temperatures in these rock pools, our results showing resilience of intertidal corals to high and variable temperatures are supported by the survival of intertidal corals after the 1997/1998 El Nino [8, 37]. Taxa which persist in these pools may be more suited to survival under future climate change scenarios, and may provide an indication of the type of community assemblages expected as global warming continues.

Aside from temperature, a major determinant of coral distribution is the amount of light available, with winter irradiance in particular constraining the latitudinal and depth ranges of some coral species [38]. Although figures for winter irradiance along the coast of KwaZulu-Natal are not available, mean annual irradiance declines from 1768 kWh/m² at Sodwana Bay to 1629 kWh/m² at Munster (data from Geosun Africa). Irradiance thus may play a role in the lower coral species richness observed at Munster, although further measurements would be needed to confirm this. Some coral species may extend their ranges by supplementing autotrophic nutrition with heterotrophic feeding [38, 39]. At least two of the coral species found at Munster, *A. irregularis* and *P. verrucosa* do so (K. Smit, unpublished data), however data are not available for the other species and we cannot ascribe their presence there to their modes of nutrition. Finally, other species-specific factors such as larval dispersal potential, which could limit the distribution of species along the coast, could not be accounted for in this study.

In summary, the hypothesis of this study is rejected. An array of hard corals persists in marginal intertidal rock pools along the coast of KwaZulu-Natal. The constant mean temperatures of rock pools suggest that temperature does not play an important role in determining the southern distribution limit of these species. The role of microhabitats in the intertidal zone has been emphasised [40–42]. The absence of a strong temperature gradient in rock pools along the coast and the relatively high water temperature in pools, especially at the southern extent of the study, potentially allow microhabitats where a diverse assemblage of hard corals can survive grow and reproduce. These conditions seem to favour some species, especially *P. verrucosa* and *A. irregularis*. Other factors, such as irradiation levels and species traits, including the degree to which species feed heterotrophically, may also influence their distributions. Understanding how these corals survive may help to understand general patterns of adaptation and acclimatisation of corals to thermal and other physical stresses.

Abbreviations

KZN: KwaZulu-Natal; SST: sea surface temperature; Fig: figure; UKZN: University of KwaZulu-Natal; NRF: National Research Foundation.

Authors' contributions

KS was responsible for the study design, data collection, analysis and interpretation of the data and write-up of the manuscript. DG assisted with data collection and interpretation of the data and assisted with the writing. Both authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets during and/or analysed during the current study available from the corresponding author on reasonable request.

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