Discovery of populations endemic to a marine biogeographical transition zone

Tirupathi Rao Golla | Leishe Pieterse | Candice M. Jooste | Peter R. Teske

Abstract

Aim: Biogeographical transition zones are areas of overlap between the faunas of adjacent biogeographical entities. Particularly the well-defined transition zones along linear coastlines are interesting natural laboratories to study dispersal and incipient speciation. Few studies have explored whether marine biogeographical transition zones harbour biodiversity that is distinct from that of the biogeographical entities they separate. The Wild Coast in eastern South Africa is a poorly studied transition zone between the region's warm-temperate and subtropical faunas, and is generally considered to be an area of faunal overlap.

Location: The South African portion of the Western Indian Ocean.

Methods: Sequences of the DNA barcoding marker COI were generated from 306 estuarine sandprawns (Kraussillichirus kraussi) collected at 13 sites. Genetic structure and evolutionary history were assessed using a haplotype network and a Bayesian discrete phylogeographic analysis.

Result: Two populations were identified whose ranges are centred on the Wild Coast, a rare one in the northern portion and a more common one in the central and southern portion of this biogeographical transition zone. These populations are not closely related to each other, but descend from subtropical and warm-temperate sister populations, respectively. Although genetic distances between populations were low, they exceeded within-population distances, indicating the presence of a "barcoding gap."

Conclusions: This is the first study to indicate that the Wild Coast marine biogeographical transition zone is not merely an area of faunal overlap, and one of very few studies to have discovered genetically unique populations within a marine biogeographical transition zone. The Wild Coast may harbour additional unique biodiversity that remains to be discovered, including rare species that require protection. More research is required to understand how this environmentally dynamic marine biogeographical transition zone differs from the adjacent biogeographical provinces.
1 | INTRODUCTION

Biogeographical transition zones are areas located between the distribution ranges of two or more independently evolving biotic entities (e.g., biogeographical regions, provinces, biomes or communities), whose intermediate environmental conditions allow overlap of faunal elements, but prevent the extension of their ranges into each other (Ferro & Morrone, 2014). They may be found in locations with either strong environmental gradients or “ribbons” of relatively unsuitable habitats (Glor & Warren, 2011), and they often have high biodiversity because of the co-occurrence of species from the adjacent biogeographical entities (Morrone, 2006; Ortega & Arita, 1998; Silva-Pereira, Meira-Neto, Rezende, & Eisenlohr, 2020). On the other hand, as the gradients in environmental and associated ecological conditions represent “filters” that limit the dispersal of biotic components into the transition zone and beyond (Simpson, 1965), biodiversity may be low when conditions in the transition zone are challenging for species from the neighbouring species assemblages (Pielou, 1992).

Many species exist whose ranges span multiple biogeographical units and the transition zones separating them (Teske, von der Heyden, McQuaid, & Barker, 2011). In these species, environmental clines are often mirrored by genetic clines (Riginos, Douglas, Jin, Shanahan, & Treml, 2011; Sokta, Wares, Barth, Grosberg, & Palumbi, 2004; Teske et al., 2011). This suggests that such widespread species in fact comprise multiple unique regional populations that are each on their own evolutionary trajectory, making biogeographical transition zones interesting areas for exploring incipient speciation and its environmental drivers (Dawson, 2005; Sommer, Harrison, Beger, & Pandolfi, 2014; Teske et al., 2019).

While many studies have explored the role of biogeographical transitions in separating populations or species, the question whether the unique environmental conditions within transition zones may harbour unique biodiversity has received comparatively little attention. Some transition zones, including the area around Wallace’s Line or the South American transition zone, can be extensive and harbour endemic species (Ferro & Morrone, 2014; Mayr, 1944; Tänzler, Toussaint, Suhardjono, Balke, & Riedel, 2014), but these are often difficult to study because they have complex geological or climatic histories (Darlington, 1957; Woodruff, 2003), and they may themselves contain multiple smaller-scale biogeographical units (Ferro & Morrone, 2014).

Marine biogeographical transition zones that are located on linear coastlines tend to have environmental gradients and associated biotic patterns that are particularly well defined. Examples of such transition zones have been reported from the south-eastern Pacific (Hormazabal, Shaffer, & Leth, 2004; Tapia, Largier, Castillo, Wieters, & Navarrete, 2014), California and Florida (Pelc, Warner, & Gaines, 2009), north-western France (Gallon et al., 2014) and along the coast of South Africa (Teske et al., 2011). These typically have well-defined gradients in sea-surface temperature, salinity and other environmental parameters.

In marine transition zones where species turnover is associated with abrupt environmental changes or unsuitable habitat, limited space makes the presence of endemic species unlikely. The present study explored the issue of endemicity in a more extensive marine biogeographical transition zone, the Wild Coast in eastern South Africa. This transition zone separates the subtropical Natal province on the east coast from the warm-temperate Agulhas province on the south coast and is characterized by a north-to-south temperature gradient resulting from the warm, southward-flowing Agulhas Current being gradually deflected away from the coast by the widening continental shelf. The transition zone is extensive and stretches over several hundred kilometres, although there is disagreement concerning the exact boundaries between the marine biogeographical provinces in this area (Lombard, 2004; Spalding et al., 2007; Teske et al., 2011; von der Heyden, 2009). Based on species turnover, the distinctiveness of this region’s fauna is only weakly supported (Emanuel, Bustamante, Branch, Eekhout, & Odendaal, 1992; Turpie & Clark, 2007), and there are no prior records of endemic species (Jooste, Oliver, Emami-Khoyi, & Teske, 2018). This study reports the first evidence for genetically distinct populations whose ranges are limited to the Wild Coast transition zone.

2 | METHODS

The study species, *Kraussillichirus kraussi* (Stebbing, 1900), is commonly known as sandprawn and was referred to in the recent literature as *Callichirus kraussi* or *Callianassa kraussi*. It is a widespread thalassinid decapod crustacean that ranges from the cool-temperate South African west coast on the Atlantic Ocean to the tropical south-western Indian Ocean (Branch, Griffiths, Branch, & Beckley, 2010; Teske, Winker, McQuaid, & Barker, 2009). The sandprawn comprises at least four phylogenetically distinct evolutionary lineages whose ranges are confined to the region’s temperature-defined marine biogeographical provinces (Teske et al., 2009), suggesting that these could be uniquely adapted cryptic species. Although its dispersal potential is low because the adults live in burrows and the non-planktonic larvae grow up in the parent burrow (Forbes, 1973), this species is exceptionally common, and one of the dominant intertidal invertebrates in the lower reaches of the region’s estuaries and sheltered marine habitats (Day, 1981; Hanekom, Baird, & Erasmus, 1988; Hanekom & Russell, 2015).

A total of 306 sandprawns were collected from 13 sites in eastern South Africa, a sampling range that includes the eastern portion
of the Agulhas province, the Wild Coast transition zone and the complete Natal province (Table 1). After removal of the smaller of the two first chelae, the prawns were released. Muscle tissue from the chela was immediately placed into CTAB extraction buffer containing proteinase K, and the extraction procedure was completed in the laboratory using the CTAB protocol (Doyle, 1991). A portion of the mitochondrial cytochrome oxidase c subunit I (COI) was amplified using forward primer CrustCOIF and reverse primer PeracCOIR, as described previously (Teske et al., 2009). Sequences were aligned in MEGA7 (Kumar, Stecher, & Tamura, 2016) and trimmed to a length of 570 bp.

Genealogical relationships between COI haplotypes were assessed by constructing a minimum-spanning network in popArt 1.7 (Leigh & Bryant, 2015). The program BEAST 2.6.2 (Bouckaert et al., 2014) was used to conduct a discrete phylogeographic analysis (Lemey, Rambaut, Drummond, & Suchard, 2009) to reconstruct the location states of ancestral branches. A maximum clade credibility tree was reconstructed using $10^8$ iterations, with trees saved every $10^4$ iterations. A COI mutation rate of 1.4% per million years was specified (Knowlton & Weigt, 1998), the HKY model (Hasegawa, Kishino, & Yano, 1985) was selected based on the Bayesian Information Criterion in MEGA, and default settings were used for all other parameters. The run was repeated twice to check for consistency of results. Following assessment of convergence and effective sample size (ESS) values in Tracer 1.7 (Rambaut, Drummond, Xie, Baele, & Suchard, 2018), the first 10% of trees were removed as burn-in in TreeAnnotator, and a phylogenetic tree constructed using median heights was visualized in FigTree 1.4.3 (Rambaut & Drummond, 2012). The program MEGA7 was used to calculate mean and minimum Kimura 2-Parameter distances (Kimura, 1980) between regional genetic clusters identified using the haplotype network and the maximum clade credibility tree, and these were compared with mean within-lineage distances. The data were also explored for the presence of a “barcoding gap” (Meyer & Paulay, 2005) by calculating a suitable distance threshold at which the number of false positives and false negatives is lowest in Spider v1.1–5 (Brown et al., 2012). As the number of sequences for this programme is limited to 200, we removed the three northernmost sites and the two southernmost sites (1–3 and 12–13, Table 1), but included all migrants. Following some exploratory runs, the starting threshold was set to 0 and the end threshold to 0.01, with intermediate thresholds explored at increments of 0.0001.

### RESULTS

Four evolutionary lineages were identified, each of which occupies a distinct portion of the coast and has a single numerically dominant haplotype (Figure 1). The warm-temperate Agulhas Province and the subtropical Natal Province each have a single lineage, and two lineages were found in the Wild Coast transition zone. Interestingly, the Wild Coast lineages were not closely related to each other (Figure 2), but are derived from the subtropical and warm-temperate lineages, respectively (Figure 3). The maximum clade credibility tree depicts

| Entity          | Site no. | Site name               | GPS coordinates          | N  |
|-----------------|----------|-------------------------|--------------------------|----|
| Natal Province  | 1        | Richards Bay Estuary     | 28°47′50″S, 32°05′14″E    | 29 |
|                 | 2        | Little Manzimtoti (Durban)| 30°04′41″S, 30°52′19″E   | 17 |
|                 | 3        | Mtentweni (Port Shepstone)| 30°42′32″S, 30°28′53″E  | 9  |
|                 | 4        | Mpenjati (Port Edward)  | 30°58′02″S, 30°16′35″E   | 18 |
| Wild Coast      | 5        | Mkazi (Cathedral Rock)   | 31°26′48″S, 29°45′43″E   | 20 |
|                 | 6        | Mbotyi                  | 31°27′51″S, 29°44′06″E   | 29 |
|                 | 7        | Bulolo (Port St Johns)  | 31°39′00″S, 29°30′59″E   | 25 |
|                 | 8        | Cintsa (East London)    | 32°49′55″S, 28°06′50″E   | 25 |
|                 | 9        | Great Fish              | 33°29′33″S, 27°07′43″E   | 27 |
| Agulhas Province| 10       | Swartkops (Port Elizabeth)| 33°52′09″S, 25°37′45″E  | 29 |
|                 | 11       | Kabeljous (Jeffreys Bay)| 34°00′18″S, 24°55′51″E   | 26 |
|                 | 12       | Keurbooms (Plettenberg Bay)| 34°02′43″S, 23°22′41″E | 26 |
|                 | 13       | Gourits                 | 34°20′15″S, 21°52′36″E   | 26 |

Note: Sites were assigned to three biogeographical entities.
a sequence of evolutionary events that started with a split into a northern lineage (red) and a southern lineage (blue). Each of these subsequently gave rise to a Wild Coast lineage in the region closest to it, one in the north (yellow) and the other in the south (green). Subsequent southward dispersal into adjacent regions (indicated by arrows) is evident in three cases. Mean and minimum genetic distances between the four regional evolutionary lineages were low, but in all cases exceeded within-lineage distances (Table S1). The most suitable genetic distance threshold to identify a barcoding gap was 0.0008 (Figure S1).

4 | DISCUSSION

Marine biogeographical transition zones are often located in areas where oceanographic conditions may create steep environmental gradients that are intermediate between those of the biogeographical provinces they separate. For many species, they represent range edges where abiotic conditions are at the extremes of their environmental niche tolerance ranges (Sagarin & Gaines, 2002). With the majority of organisms that disperse into these regions being physiologically maladapted, there are clear selective advantages for local populations to adapt to these conditions, but the identification of endemic biodiversity is not usually a primary aim when studying biogeographical transitions. Comprehensive taxonomic or genetic research can potentially elevate the status of transition zones from areas of range overlap to regions whose unique biodiversity makes them priority areas for management and conservation.

An example of another African marine biogeographical transition zone, located on the south-west coast of South Africa and separating cool-temperate Atlantic Ocean fauna from warm-temperate Indian Ocean fauna, presents a case in point. While older literature considered it to be a region of overlap (Brown & Jarman, 1978; Day, 1969), it is now treated as a distinct coastal biogeographical province, the “South-western Cape Bioregion” (Lombard, 2004). This status is also supported by the presence of local, genetically distinct populations of more widespread species that may represent cryptic species (Teske et al., 2011; von der Heyden, 2009).

The Wild Coast marine biogeographical transition zone has similarly been treated as a region of faunal overlap (Day, 1981; Harrison, 2002), although some studies, using community analysis, have found weakly differentiated clusters (Emanuel et al., 1992; Turpie & Clark, 2007). Similarly, most genetic studies have found extensive range overlap between sister lineages of temperate and subtropical species in this region (Teske et al., 2008; Zardi, McQuaid, Teske, & Barker, 2007). Evidence for endemicity was so far limited to distinct genetic clusters rather than taxonomically described morphospecies (Jooste et al., 2018), but, even for these, the evidence was not strong. The rocky shore limpets Scutellastra barbara and S. longicosta had south-east coast lineages whose ranges approximately matched that of the Kraussillichirus kraussi lineage from the Central and Southern Wild Coast (Mmonwa, Teske, McQuaid, & Barker, 2015). However, the fact that the area sampled for both species excluded the subtropical Natal Province, where both are present (Branch et al., 2010), suggests that the Wild Coast may merely be the southern distribution limit of more widespread evolutionary lineages. The prawn Palaemon capensis showed unique mtDNA-based population structure in the southern Wild Coast, but no distinct lineages were found, and this result may be an artefact of range-wide isolation by distance (Wood, Grave, & Daniels, 2017). At the southern edge of the transition zone, a genetically distinct site was found in the brown mussel Perna perna using microsatellite data, but this was not
confirmed with mtDNA sequence data (Ntuli et al., 2020). Similarly, a unique Wild Coast cluster of genomic loci under thermal selection was found in an endemic goby (Teske et al., 2019), but, again, this region did not have a distinct mtDNA lineage (Drost, Golla, von der Heyden, & Teske, 2016). Mean genetic distances between the four regional evolutionary lineages of *Kraussillichirus kraussi* identified in this study are below commonly used fixed distance thresholds of \(-0.01–0.02\) (i.e. \(1\%–2\%\)) for DNA barcoding of crustaceans (Bezeng & van der Bank, 2019; Raupach et al., 2015). Based on this criterion, the lineages would thus not be considered to be distinct species. On the other hand, the fact that within-lineage genetic distances were consistently smaller than minimum between-lineage distances indicates the existence of a "barcoding gap" (Meyer & Paulay, 2005), and justifies the application of a lower distance threshold to delineate populations. This, and the clearly defined geographical ranges of each of the four lineages, provides the first evidence for endemic diversity within the Wild Coast transition zone.

Some dispersal into adjacent bioregions, likely driven by the southward-flowing Agulhas Current, was evident, and exploring whether individuals from different mtDNA lineages that were found at the same sites can hybridize presents an interesting future endeavour. *Kraussillichirus kraussi* is not a suitable candidate for traditional taxonomy because its morphology is highly conserved, and even individuals from the species' genetically highly divergent tropical population (Teske et al., 2009) are not distinguishable from the south coast population (Peter Dworschak, Naturhistorisches Museum Wien, pers. comm.). However, in addition to the mtDNA-based genetic differences identified here, there may be physiological adaptations that differ between populations and limit the amount of admixture between regions. For example, subtropical sandprawns can osmoregulate more efficiently than their warm-temperate counterparts, particularly at

![FIGURE 2](image_url)  
A minimum-spanning haplotype network of the COI haplotypes of *Kraussillichirus kraussi*. Each circle represents a unique haplotype, and the size of each circle reflects the haplotype’s frequency. Connecting branches represent single nucleotide differences between haplotypes. Colours in this case were used to assign haplotypes to four sections of coastline (Table 1). Site numbers (which correspond to those in Figure 1) are shown in white squares. Haplotypes were assigned to four evolutionary lineages (A–D). These closely match the four sections of coastline, as each lineage is dominated by haplotypes from a specific biotic entity (A: Natal Province, B: Northern Wild Coast, C: Central and Southern Wild Coast, D: Agulhas Province), but the lineages also include migrants from other regions.

![FIGURE 3](image_url)  
Bayesian maximum clade credibility tree constructed from COI sequences of the sandprawn *Kraussillichirus kraussi*. Colours represent four sections of coastline (see Figure 2), with internal branches indicating the most likely geographical location of a branch in the past, and the scale at the bottom indicating the approximate time of divergence. Four evolutionary lineages were identified, whose ranges are centred on a specific portion of the coastline (A: Natal Province, B: Northern Wild Coast, C: Central and Southern Wild Coast, D: Agulhas Province), but which also include migrants from other regions (indicated by arrows), i.e. individuals that are nested within lineages that are numerically dominated by individuals from other regions.
lower salinities (Cerff, 1986; Forbes, 1974), which may be an adaptation to the combination of greater precipitation and less seawater input into east coast estuaries (Teske et al., 2009). Wild Coast prawns may have intermediate osmoregulatory abilities, in addition to being adapted to a unique thermal environment, as shown for other species from this region (Papadopoulos & Teske, 2014; Teske et al., 2008, 2019; Zardi, Nicastro, McQuaid, Hancke, & Helmuth, 2011). Hence, although mtDNA-based divergence of the Wild Coast populations is minimal, gene regions that are involved in environmental adaptation may already be much more divergent (Teske et al., 2019).

The data generated here are not considered suitable for inferring what oceangraphical conditions existed along the Wild Coast during the time when the regional populations split from their sister taxa. This is because mtDNA is often under strong selection (Meiklejohn, Montooth, & Rand, 2007; Stewart, Freyer, Elson, & Larsson, 2008) and thus violates the assumption of the neutral theory of evolution (Kimura, 1983), which makes its usefulness for molecular dating questionable (Matumba, Oliver, Barker, McQuaid, & Teske, 2020). Our maximum clade credibility tree indicates that the splits may have occurred during the previous interglacial phase (~120,000 years ago) or during the subsequent glacial phase, although potential diversifying selection linked to thermal selection suggests that divergence could have taken place more recently. Genetic patterns that evolved earlier are nonetheless likely maintained by contemporary environmental conditions. The rare genetic lineage that was dominant at site 6 is likely affected by a semi-permanent cyclonic eddy reported in this area (Roberts, van der Lingen, Whittle, & van den Berg, 2010), which may limit long-distance dispersal. Its location south of a coastal indent that limits the impact of the warm Agulhas Current may result in reduced influx of migrants from the northern lineage, while also reducing nearshore temperatures. Similarly, mixing between the southern Wild Coast lineage and its warm-temperate sister lineage may result in reduced influx of migrants from the northern lineage, while also reducing nearshore temperatures. Similarly, mixing between the southern Wild Coast lineage and its warm-temperate sister lineage may be limited by the widening of the continental shelf in this area, which reduces the direct influence of the Agulhas Current, and generates a nearshore countercurrent and strong upwelling (Lutjeharms, Cooper, & Roberts, 2000).

5 | CONCLUSION

Despite its importance as a biogeographical transition zone that limits the southward dispersal of Western Indian Ocean fauna into the temperate biogeographical provinces at the southern tip of Africa, the Wild Coast has received comparatively little scientific attention. The present study represents a significant advancement in that regard, and rejects the finding of a previous study that tentatively rejected the idea that the Wild Coast has endemic biodiversity (Jooste et al., 2018). Given the very small range of the northern Wild Coast lineage, a fine-scale sampling approach is clearly required to properly document the biodiversity of this poorly studied region, and determine whether the spatial genetic patterns found here are unique to K. kraussi or represent a more general phenomenon. Several estuarine species of high conservation priority that occur elsewhere in South Africa have very small distribution ranges (Allanson, 1958; Penrith & Penrith, 1972; Whitfield, 1995; Whitfield, Mkare, Teske, James, & Cowley, 2017), and it is likely that such species also exist along the Wild Coast.

ACKNOWLEDGEMENTS

We are grateful to Sophie Bader, Alessia Dinoi and Juliana Klein for helping with the sampling. This study was supported by the PADI Foundation (Grant No. 10981) and by an FRC/URC grant from the University of Johannesburg awarded to PRT. TRG was awarded a Global Excellence and Stature (GES) doctoral fellowship, and CMJ received a grant-holder-linked MSc bursary from the NRF.

CONFLICT OF INTEREST

The authors declare they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Sequence data have been submitted to the GenBank database under accession numbers MT578899–MT579204.

ORCID

Peter R. Teske https://orcid.org/0000-0002-2838-7804

REFERENCES

Allanson, B. R. (1958). On the systematics and distribution of the molluscan genus *Siphonaria* in South Africa. *Hydrobiologia*, 12(2), 149–180. https://doi.org/10.1007/BF00034147

Bezeng, B. S., & van der Bank, H. F. (2019). DNA barcoding of southern African crustaceans reveals a mix of invasive species and potential cryptic diversity. *PLoS One*, 14(9), e0222047. https://doi.org/10.1371/journal.pone.0222047

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., ... Drummond, A. J. (2014). BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, 10(4), e1003537. https://doi.org/10.1371/journal.pcbi.1003537

Branch, G. M., Griffiths, C. L., Branch, M. L., & Beckley, L. E. (2010). Two Oceans - a guide to the marine life of southern Africa, 3rd ed...166–167. Cape Town, South Africa: Struik Nature.

Brown, A. C., & Jarman, N. (1978). Coastal marine habitats. M. J. A. Weger In *Biogeography and ecology of southern Africa*, Monographiae Biologicae(1239–1277). Dordrecht: Springer.

Brown, S. D. J., Collins, R. A., Boyer, S., Lefort, M.-C., Malumbres-Olarte, J., Vink, C. J., & Cruickshank, R. H. (2012). Spider: An R package for the analysis of species identity and evolution, with particular reference to DNA barcoding. *Molecular Ecology Resources*, 12(3), 562–565. https://doi.org/10.1111/j.1755-0998.2011.03108.x

Cerff, E. C. (1986). Salinity and temperature responses in Callianassa kraussi (Crustacea: Decapoda: Thalassinidea), MSc thesis, Durban, South Africa: University of Natal.

Darlington, P. J. Jr (1957). Zoogeography: The geographical distribution of animals, New York: John Wiley & Sons.

Dawson, M. N. (2005). Incipient speciation of *Catostylus mosaicus* (Sphyhoozoa, Rhizostomeae, Catostylidae), comparative phylogeography and biogeography in south-east Australia. *Journal of Biogeography*, 32(3), 515–533. https://doi.org/10.1111/j.1365-2699.2004.01193.x

Day, J. H. (1969). *A guide to marine life on South African shores*, Cape Town & Rotterdam: A.A. Balkema.

Day, J. H. (1981). Fauna. In *Estuarine ecology with particular reference to southern Africa* (pp. 147–178). Rotterdam: A. A. Balkema.

Doyle, J. (1991). CTAB total DNA isolation. G. M. Hewitt A. W. B. Johnston & J. P. W. Young In *Molecular techniques in taxonomy* (pp. 283–293). Berlin, Heidelberg: Springer-Verlag.
Drost, E., Golla, T. R., von der Heyden, S., & Teske, P. R. (2016). No divergent evolution, despite restricted connectivity, between Atlantic and Indian Ocean goby populations. *Marine Biodiversity, 46*(2), 465–471. https://doi.org/10.1007/s12526-015-0389-6

Emanuel, B. P., Bustamante, R. H., Branch, G. M., Eekhout, S., & Odendaal, F. J. (1992). A zogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. *South African Journal of Marine Science, 12*(1), 341–354. https://doi.org/10.2989/02577619209504710

Ferro, I., & Morrone, J. J. (2014). Biogeographical transition zones: A search for conceptual synthesis. *Biological Journal of the Linnean Society, 113*(1), 1–12. https://doi.org/10.1111/bij.12333

Forbes, A. T. (1973). An unusual abbreviated larval life in the estuarine burrowing prawn *Callianassa kraussi* (Crustacea: Decapoda: Thalassinidea). *Marine Biology, 22*(4), 361–365. https://doi.org/10.1007/BF00391395

Forbes, A. T. (1974). Osmotic and ionic regulation in *Callianassa kraussi* Stebbing (Crustacea: Decapoda: Thalassinidea). *Journal of Experimental Marine Biology and Ecology, 16*(3), 301–311. https://doi.org/10.1016/0022-0981(74)90029-X

Gallon, R. K., Robuchon, M., Leroy, B., Gall, L. L., Valero, M., & Feunteun, E. (2014). Twenty years of observed and predicted changes in subtidal red seaweed assemblages along a biogeographical transition zone: Inferring potential causes from environmental data. *Journal of Biogeography, 41*(12), 2293–2306. https://doi.org/10.1111/1365-2699.12380

Glor, R. E., & Warren, D. (2011). Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research, 20*(7), 737–761. https://doi.org/10.1016/j.csr.2010.09.002

Hanekom, N., Baird, D., & Erasmus, T. (1988). A quantitative study to assess standing biomasses of macrobenthos in soft substrata of the Swartkops Estuary, South Africa. *South African Journal of Marine Science, 6*(1), 163–174. https://doi.org/10.2989/025776188784480500

Hanekom, N., & Russell, I. A. (2015). Temporal changes in the macrobenthos of sandprawn (*Callichthys kraussi*) beds in Swartvlei Estuary, South Africa. *African Zoology, 50*(1), 41–51. https://doi.org/10.1080/15627020.2015.1021177

Harrison, T. D. (2002). Preliminary assessment of the biogeography of fishes in South African estuaries. *Marine and Freshwater Research, 53*, 479–490. https://doi.org/10.1071/MF01112

Hasegawa, M., Kishino, H., & Yano, T. (1985). Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution, 22*(2), 160–174. https://doi.org/10.1007/BF02010194

Hormazabal, S., Shaffer, G., & Lith, O. (2004). Coastal transition zone off Chile. *Journal of Geophysical Research: Oceans, 109*, C01021https://agupubs.onlinelibrary.wiley.com/doi/pdf/10.1029/2003JC001956

Jooste, C. M., Oliver, J., Emami-Khoyi, A., & Teske, P. R. (2018). Is the Wild Coast in eastern South Africa a distinct marine bioregion? *Helgoland Marine Research, 72*(2), 6. https://doi.org/10.1007/s10152-018-0509-3

Kimura, M. (1980). A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution, 16*(2), 111–120. https://doi.org/10.1007/BF01731581

Kimura, M. (1983). *The neutral theory of molecular evolution*. Cambridge: Cambridge University Press.

Knowlton, N., & Weig特, L. A. (1998). New dates and new rates for divergence across the Isthmus of Panama. *Proceedings of the Royal Society B: Biological Sciences, 265*(1412), 2257. https://doi.org/10.1098/rspb.1998.0568

Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution, 33*(7), 1870–1874. https://doi.org/10.1093/molbev/msw054

Leigh, J. W., & Bryant, D. (2015). popart: Full-feature software for haplotype network construction. *Methods in Ecology and Evolution, 6*(9), 1110–1116. https://doi.org/10.1111/2041-210X.12410

Lemey, P., Rambaut, A., Drummond, A. J., & Suchard, M. A. (2009). Bayesian phylogenetic fingerprinting its roots. *PLoS Computational Biology, 5*(9), e1000520. https://doi.org/10.1371/journal.pcbi.1000520

Lombard, A. T. (2004). Marine component of the National Spatial Biodiversity Assessment for the development of South Africa’s National Biodiversity Strategic and Action Plan, Pretoria: . National Botanical Institute.

Lutjeharms, J. R. E., Cooper, J., & Roberts, M. (2000). Testing ecological explanations for biogeographic boundaries. *Methods in Ecology and Evolution, 5*(2), 2041–2054. https://doi.org/10.1046/j.1365-2699.2000.00304.x

Memon, K., Teske, P. R., McQuaid, C., & Barker, N. (2015). Historical demography of southern African patellid limpets: Congruence of population expansions, but not phylogeography. *African Journal of Marine Science, 37*(1), 225–263. https://doi.org/10.1016/j.ajms.2010.03.008

Meyer, C. P., & Paulay, G. (2005). DNA barcoding: Error rates based on comprehensive sampling. *PLoS Biology, 3*(12), 1–10. https://doi.org/10.1371/journal.pbio.0030422

Morrone, J. J. (2006). Biogeographic areas of transition zones of the Mediterranean Sea and adjacent regions. *Marine Biodiversity, 22*(3), 465–471. https://doi.org/10.1111/j.1090-5529.2005.22010.x

Papadopoulos, I., & Teske, P. (2014). Larval development reflects biogeographic and cladistic analyses of the entomofauna. *African Journal of Marine Science, 36*(3), 476–494. https://doi.org/10.1146/annurev.eento.50.071803.130447

Nülle, N. N., Nicostratos, K. R., Zardi, G. I., Assis, J., McQuaid, C. D., & Teske, P. R. (2020). Rejection of the genetic implications of the “Abundant Centre Hypothesis” in marine mussels. *Scientific Reports, 10*(1), 1–12. https://doi.org/10.1038/s41598-020-57474-0

Ortega, J., Arita, H. T., & Arita, H. T. (1998). Neotropical-Nearctic limits in Middle America as determined by distributions of bats. *Journal of Mammalogy, 79*(3), 772–783. https://doi.org/10.2307/1383088

Pelc, R. A., Warner, R. R., & Gaines, S. D. (2009). Geographical patterns of genetic structure in marine species with contrasting life histories. *Journal of Biogeography, 36*(10), 1881–1890. https://doi.org/10.1111/j.1365-2699.2009.02138.x

Penrith, M. J., & Penrith, M. (1972). Redescription of *Pandaka silvana* (Barnard) (Pisces, Gobiidae). *Annals of the South African Museum, 60*, 105–108.

Pielou, E. C. (1992). Biogeography. Malabar:. Krieger Publishing Company.

Rambaut, A., & Drummond, A. J. (2012). *FigTree*: Tree figure drawing tool, v1.4.2. Edmonton:. University of Edinburgh.

Rambaut, A., Drummond, A. J., Xie, D., Baele, G., & Suchard, M. A. (2018). Posterior summarization in Bayesian phylogenetics using *Tracer 1.7*. *Systematic Biology, 67*(5), 901–904. https://doi.org/10.1093/sysbio/sys032

Raupach, M. J., Barco, A., Steinke, D., Beermann, J., Laakmann, S., Mohrbeck, I., … Knebelberger, T. (2015). The application of DNA barcodes for the identification of marine crustaceans from the North Sea and adjacent regions. *PLoS One, 10*(9), e0139421. https://doi.org/10.1371/journal.pone.0139421
Riggins, C., Douglas, K. E., Jin, Y., Shanahan, D. F., & Treml, E. A. (2011). Effects of geography and life history traits on genetic differentiation in benthic marine fishes. *Ecography*, 34(4), 566–575. https://doi.org/10.1111/j.1600-0587.2010.06511.x

Roberts, M. J., van der Lingen, C. D., Whittle, C., & van den Berg, M. (2010). Shelf currents, lee-trapped and transient eddies on the inshore boundary of the Agulhas Current, South Africa: Their relevance to the KwaZulu-Natal sardine run. *African Journal of Marine Science*, 32(2), 423–447. https://doi.org/10.2989/1814232X.2010.512655

Sagarin, R., & Gaines, S. (2002). The ‘abundant centre’ distribution: To what extent is it a biogeographical rule? *Ecology Letters*, 5, 137–147. https://doi.org/10.1046/j.1461-0248.2002.00297.x

Silva-Pereira, I., Meira-Neto, J. A. A., Rezende, V. L., & Eisenlohr, P. V. (2020). Biogeographic transitions as a source of high biologic diversity: Phylogenetic lessons from a comprehensive ecotone of South America. *Perspectives in Plant Ecology, Evolution and Systematics*, 44, 125528. https://doi.org/10.1016/j.pee.2020.125528

Simpson, G. G. (1965). *The geography of evolution*, Philadelphia: Chilton.

Sommer, B., Harrison, P. L., Beger, M., & Pandolfi, J. M. (2014). Trait-The geography of evolution. *Evolutionary ecology*, 38(4), 657–662. https://doi.org/10.1007/s10682-013-9719-6

Setka, E. E., Wares, J. P., Barth, J. A., Grosberg, R. K., & Palumbi, S. R. (2004). Strong genetic clines and geographical variation in gene flow in the rocky intertidal barnacle *Balanus glandula*. *Molecular Ecology*, 13(8), 2143–2156. https://doi.org/10.1111/j.1365-294X.2004.02225.x

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., … Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience*, 57(7), 573–583. https://doi.org/10.1641/B570707

Stewart, J. B., Freyer, C., Elson, J. L., & Larsson, N.-G. (2008). Purifying selection of mtDNA and its implications for understanding evolution and mitochondrial disease. *Nature Reviews Genetics*, 9(9), 657–662. https://doi.org/10.1038/nrg2396

Tänzler, R., Toussaint, E. F. A., Suhardjono, Y. R., Balke, M., & Riedel, A. (2014). Multiple transgressions of Wallace’s Line explain diversity of flightless *Trigonopterus* weevils on Bali. *Proceedings of the Royal Society B: Biological Sciences*, 281(1782), 20132528. https://doi.org/10.1098/rspb.2013.2528

Tapia, F. J., Largier, J. L., Castillo, M., Wieters, E. A., & Navarrete, S. A. (2014). Latitudinal discontinuity in thermal conditions along the nearshore of central-northern Chile. *PLoS One*, 9(10), e110841. https://doi.org/10.1371/journal.pone.0110841

Teske, P. R., Papadopoulos, I., Newman, B. K., Dworschak, P. C., McQuaid, C. D., & Barker, N. P. (2008). Oceanic dispersal barriers, adaptation and larval retention: An interdisciplinary assessment of potential factors maintaining a phylogeographic break between sister lineages of an African prawn. *BMC Evolutionary Biology*, 8, 341. https://doi.org/10.1186/1471-2148-8-341

Teske, P. R., Sandoval-Castillo, J., Golla, T. R., Emami-Khoyi, A., Tine, M., von der Heyden, S., & Beheregaray, L. B. (2019). Thermal selection as a driver of marine ecological speciation. *Proceedings of the Royal Society B: Biological Sciences*, 286(1896), 20182023. https://doi.org/10.1098/rspb.2018.2023

Teske, P. R., von der Heyden, S., McQuaid, C. D., & Barker, N. P. (2011). A review of marine phylogeography in southern Africa. *South African Journal of Science*, 107(S6), 1–11. https://doi.org/10.4102/sajs.v107i6.514

Teske, P. R., Winker, H., McQuaid, C. D., & Barker, N. P. (2009). A tropical/subtropical biogeographic disjunction in southeastern Africa separates two evolutionarily significant units of an estuarine prawn. *Marine Biology*, 156(6), 1265–1275. https://doi.org/10.1007/s00227-009-1168-3

Turpie, J. K., & Clark, B. (2007). Development of a conservation plan for temperate South African estuaries on the basis of biodiversity importance, ecosystem health and economic costs and benefits (C.A.P.E. Regional Estuarine Management Programme, p. 125). Anchor Environmental Consultants CC.

von der Heyden, S. (2009). Why do we need to integrate population genetics into South African marine protected area planning? *African Journal of Marine Science*, 31(2), 263–269. https://doi.org/10.2989/AJMS.2009.31.2.14.886

Whitfield, A. K. (1995). Threatened fishes of the world: *Hippocampus capensis* Boulenger, 1900 (Syngnathidae). *Environmental Biology of Fishes*, 44(4), 362. https://doi.org/10.1007/BF00008251

Whitfield, A. K., Mkare, T. K., Teske, P. R., James, N., & Cowley, P. D. (2017). Life-histories explain the conservation status of two estuary-associated pipefishes. *Biological Conservation*, 212, 256–264. https://doi.org/10.1016/j.biocon.2017.06.024

Wood, L. E., Grave, S. D., & Daniels, S. R. (2017). Phylogeographic patterning among two codistributed shrimp species (Crustacea: Decapoda: Palaeonidae) reveals high levels of connectivity across biogeographic regions along the South African coast. *PLoS One*, 12(3), e0173356. https://doi.org/10.1371/journal.pone.0173356

Woodruff, D. S. (2003). Neogene marine transgressions, palaeogeography and biogeographic transitions on the Thai-Malay Peninsula. *Journal of Biogeography*, 30(4), 551–567. https://doi.org/10.1046/j.1365-2699.2003.00846.x

Zardi, G. I., Nicastro, K. R., McQuaid, C. D., Hancke, L., & Helmut, B. (2011). The combination of selection and dispersal helps explain phylogeographic structure in intertidal mussels. *Oecologia*, 165(4), 947–958. https://doi.org/10.1007/s00442-010-1788-9

**BIOSKETCH**

Tirupathi Rao Golla is a postdoctoral researcher who uses molecular methods to understand genetic structure in marine areas that lack absolute dispersal barriers. Leishe Pieterse and Candice Jooste worked on the data used for this manuscript as part of their Bsc honours and MSc projects, respectively. Peter Teske is a researcher at the University of Johannesburg who uses molecular methods to detect overlooked biodiversity, with the aim of improving the management of exploited or threatened species.

**AUTHOR CONTRIBUTIONS:** P.R.T. conceived the research and supervised the other authors; T.R.G. and P.R.T. collected the samples; L.P., C.M.J. and T.R.G. generated the data; L.P., C.M.J., T.R.P. and P.R.T. analysed the data; and T.R.P. and P.R.T. wrote the manuscript.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Golla TR, Pieterse L, Jooste CM, Teske PR. Discovery of populations endemic to a marine biogeographical transition zone. *Divers. Distrib.*

2020;26:1825–1832. https://doi.org/10.1111/ddi.13162