

ORIGINAL ARTICLE

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Is the Wild Coast in eastern South Africa a distinct marine bioregion?

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Abstract

The South African coastline can be divided into at least four temperature-defined marine bioregions, including the tropical north-east coast, the subtropical east coast, the warm-temperate south coast, and the cool-temperate west coast. There are also two biogeographical transition zones, the south-west coast and the south-east coast (or Wild Coast). The former is sometimes considered a distinct marine bioregion, but no such status has yet been suggested for the Wild Coast. Previous data on the distribution of a recently described but very common coastal crab, *Hymenosoma longicrure*, indicated that this species could be a Wild Coast endemic. If confirmed, this would be a first indication that this region harbours unique fauna, and that additional research is required to determine whether the Wild Coast constitutes a distinct bioregion that needs to be managed separately from other coastal regions. In the present study, we generated novel genetic data for *H. longicrure* and compared the species' range with that of its southern African congeners. We found that *H. longicrure* occurs north of the Wild Coast, where its range overlaps with that of *H. projectum*. This finding rejects the idea that the Wild Coast harbours endemic fauna and suggests that the ranges of the two species may be linked to the subtropical and tropical bioregions, respectively, with some southward dispersal facilitated by the southward-flowing Agulhas Current. We conclude that there is as yet no compelling evidence that the Wild Coast is a distinct marine bioregion, and concur with previous biogeographical studies which have suggested that the Wild Coast is an area in which species from the subtropical and warm-temperate bioregions have overlapping ranges. Nonetheless, that fact that no biological information is available for the majority of the region's estuaries highlights the necessity of comprehensively documenting the biodiversity of this understudied region to fully resolve this issue.

Keywords: Biogeography, Crab, Endemic species, Marine biodiversity, South Africa, Transition zone, Wild Coast

Background

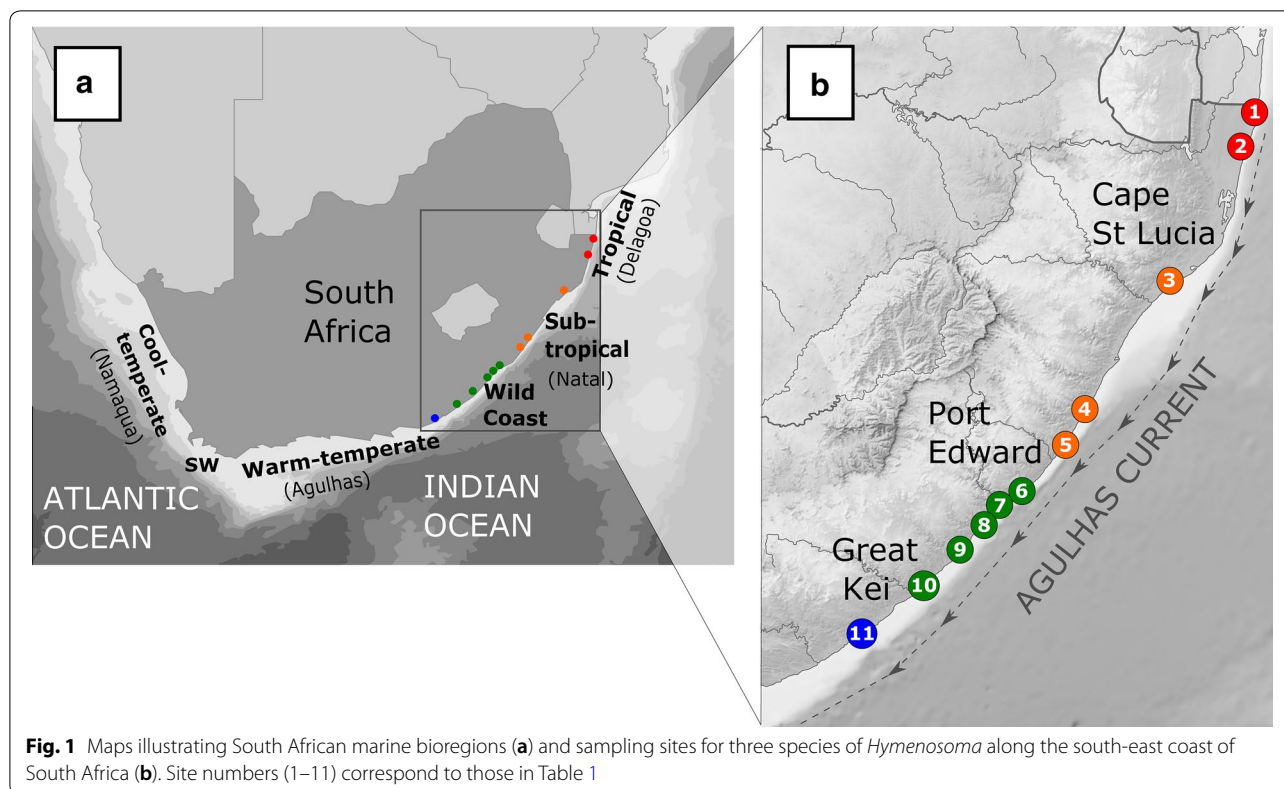
The coastline of South Africa is exceptionally diverse. Located at the contact area of the Atlantic and Indian Ocean biomes, it not only comprises biotic elements from two oceans [1], but there are also large numbers of endemics [2–4]. Environmental conditions change considerably from west to east and based on species assemblage data, most authors have accepted three major temperature-defined coastal marine biogeographical regions, including the cool-temperate Namaqua bioregion in the west, the warm-temperate Agulhas bioregion

in the south, and the subtropical Natal bioregion in the east [2, 5–7] (Fig. 1). Genetic data indicate that the boundaries between these marine bioregions are mirrored below the species level, as numerous cryptic sister species that are morphologically difficult to distinguish have been found in adjacent bioregions [8].

Several recent studies have suggested that there is also a tropical region in the north-east (the Delagoa bioregion [3, 9]; Fig. 1), and genetic data strongly support this [8, 10–13]. There are also two major biogeographical transition areas whose status as bioregions is less clear. The region between the two temperate bioregions in the south-west has been treated as a transition zone in the older literature [14–16], but more recently it has been referred to as the South-western Cape bioregion [3]. Although the distinctness of the region from

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the temperate bioregions has been confirmed by some genetic studies based on endemic cryptic species [17–21], there is considerable disagreement about its exact location [3, 8, 20].

The status of the other transition zone (located between the warm-temperate and subtropical bioregions) as a distinct bioregion is less strongly supported. This region, which is known as the Wild Coast and is roughly located between the Great Kei River and Port Edward (Fig. 1), has been described as an area rich in species endemic to South Africa [2] and there are distinct faunal discontinuities that include a rapid increase in the proportion of warm-water rocky shore species north of Port St Johns [21] and a distinct change in sandy beach macrofauna [22]. Based on community data, some authors have grouped the Wild Coast with the warm-temperate south coast [2] while others have grouped it with the subtropical east coast [6, 23], or found conflicting affinities depending on the methods used [9].

While some studies using species assemblage data found that Wild Coast sites formed distinct but weakly differentiated clusters [2, 5], the strongest support for the distinctness of this region comes from genetic data: the limpets *Scutellastra barbara* and *S. longicosta* [24] both have unique south-eastern lineages in this region, and there is also a south-eastern lineage of the shrimp

Palaemon capensis [25], although its range is slightly south of that described above. So far, there is only one example of a taxonomically described species that may be endemic to the Wild Coast: the coastal crown crab *Hymenosoma longicrure* [26]. This species was previously referred to as *H. orbiculare* [27], but it was identified as a distinct cryptic species based on genetic data, together with one more coastal crown crab (*H. projectum* [26]) and two deeper-water species (*H. trilobatum* [26] and *H. geometricum* [28]) that were also formerly lumped with *H. orbiculare* [13, 29, 30]. Subsequent morphological analyses confirmed their species status [26]. The South African distribution records of *H. orbiculare*, *H. longicrure* and *H. projectum* indicate links with distinct coastal areas, with *H. orbiculare* being present throughout the temperate regions, *H. longicrure* along the Wild Coast, and *H. projectum* in the subtropical and tropical regions [12, 13, 26, 29, 31–34].

The fact that many species in eastern South Africa often occur far outside their normal ranges because they are transported southwards by the Agulhas Current [33], and numerous species migrate northwards [34], may have made it difficult to clearly identify this region as distinct because resident species are outnumbered by migrants. The identification of endemics that are adapted to the intermediate temperatures of the Wild Coast would

provide support for its status as a distinct bioregion, in the same way the south-west coast is now treated as such [3]. In the present study, the distribution of the three coastal species of *Hymenosoma* was re-assessed using data from additional sampling sites, with the specific aim of confirming that *H. longicrura* is indeed a Wild Coast endemic. Given the difficulties involved in distinguishing the three species in the field, genetic methods were used to verify their identity.

Materials and methods

Genetic data generation

Samples were collected from estuaries located on the Wild Coast and in the subtropical marine bioregion (Table 1) using a D-frame net. Each specimen had one leg removed and placed into an Eppendorf tube containing 10 µl of Proteinase K and 180 µl of CTAB Buffer [35], after which the specimen was released. The samples were taken back to the laboratory within a week of collection, and additional Proteinase K was added every 2 days to prevent the growth of microbes, for a total of 20 µl of Proteinase K. DNA extraction was then completed in the laboratory using the CTAB method [35]. The data generated were supplemented with data from previous studies for a total of 11 study sites ranging from the tropical to the warm-temperate bioregions [13, 32].

Table 1 Sampling locality information with coordinates and specific marine bioregions in which samples were collected

Site no.	Site name	Coordinates	Bioregion	No. sequences
1	kuHlange	26°54'42"S; 32°52'00"E	Tropical	7
2	Lake Sibaya	27°24'24"S; 32°42'09"E	Tropical	2
3	Mzingazi	28°47'44"S; 32°04'15"E	Subtropical	10
4	Mzimkhulu	30°44'59"S; 30°27'01"E	Subtropical	35*
5	Mpenjati	30°58'19"S; 30°17'02"E	Subtropical	2+6*
6	Mntafufu	31°33'49"S; 29°38'10"E	Wild Coast	31*
7	Mzimvubu	31°37'18"S; 29°33'04"E	Wild Coast	4
8	Mngazana	31°41'29"S; 29°25'24"E	Wild Coast	54*
9	Mbhanyana	32°13'41"S; 28°55'43"E	Wild Coast	57*
10	Qolora	32°37'49"S; 28°25'59"E	Wild Coast	47
11	Gqunube	32°55'53"S; 28°01'45"E	Warm-temperate	30

The asterisks indicate novel sequences generated for this study

The cytochrome oxidase *c* subunit I gene (COI) was amplified using universal primers LCO1490: 5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3' (forward) and HC02198: 5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3' (reverse) [36]. Polymerase chain reactions (PCR) were performed in reaction volumes of 15 µl containing the following reagents: 6.64 µl of double-distilled water, 1.2 mM of MgCl₂ and 2 µl of 10 × PCR Buffer (Promega), 1 mM of dNTPs (Sigma-Aldrich), 0.5 mM of each primer, 1 µl of BSA, 0.16 µl of Super-Therm Taq polymerase (5 units µl⁻¹; Separation Scientific, South Africa), and 2 µl of DNA template. The following cycling profile was used: an initial denaturation step (2 min at 94 °C), 40 cycles of denaturation (30 s at 94 °C), annealing (45 s at 50 °C), extension (1 min at 72 °C), and a final extension step (10 min at 72 °C). Successful amplification was verified via gel electrophoresis on a 2% agarose gel. Sequencing was performed using a BigDye Terminator v3.1 Cycle Sequencing Kit, and reactions were run on an ABI 3730 DNA analyser (Applied Biosystems). Sequences were aligned and edited with the program MEGA v.6 [37], and a median joining haplotype network [38] was constructed using PopART [39].

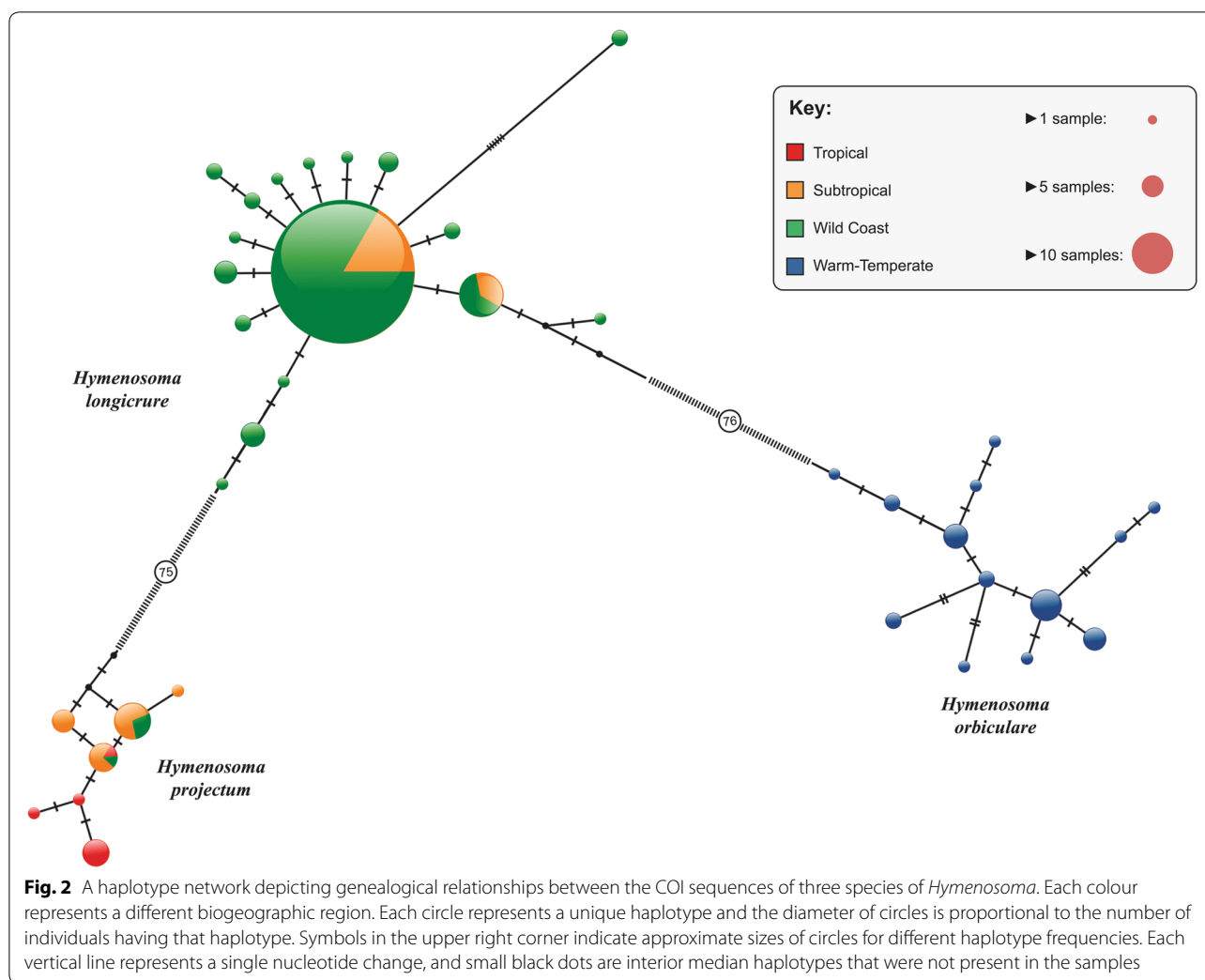
Results

The final data set comprised 285 COI sequences, including 31 sequences of *Hymenosoma projectum*, 224 sequences of *H. longicrura*, and 30 sequences of *H. orbiculare*. From these sequences, 37 unique haplotypes were recovered. In the haplotype network (Fig. 2) sequences of *H. longicrura*, *H. projectum*, and *H. orbiculare* were recovered as three distinct clusters. Samples of *H. projectum* were found in the tropical and subtropical bioregions and on the Wild Coast, samples of *H. longicrura* were present in the subtropical region as well as along the Wild Coast, and samples of *H. orbiculare* were not found north of the warm-temperate bioregion (Fig. 3). Although the ranges of *H. projectum* and *H. longicrura* overlapped, each site had only a single species.

Discussion

This study re-investigated the distribution ranges of three species of crown crab along the eastern coastline of South Africa, with a specific focus on the subtropical marine bioregion and the understudied Wild Coast. It was found that *H. projectum* and *H. longicrura* are not strictly confined to specific portions of the coast, as previously believed [13, 26, 29, 32]. *Hymenosoma longicrura* is not a Wild Coast endemic but is also represented in the subtropical bioregion to the north.

The ranges of planktonic larval dispersers in southern Africa tend to be linked to the region's temperature-defined marine bioregions [8]. The finding that *H.*



longicrure is not endemic to the Wild Coast can potentially be explained by the range of this species comprising the entire region considered to be subtropical by some authors [5, 23, 40, 41], including the Wild Coast (but see [2]). Similarly, *H. projectum* could be primarily a tropical species that has established itself in some estuaries outside its normal range as a result of southward transport by the Agulhas Current. Occurrences of species south of their primary ranges have been reported for numerous other species along much of the east coast [33]. This would suggest that specimens from Mozambique identified as *H. orbiculare* [42, 43], and perhaps even from Zanzibar [44], were most likely specimens of *H. projectum* in their northern, tropical range.

With the exception of a genetic study of the limpets *Scutellastra barbara* and *S. longicosta* which, like previous studies on *Hymenosoma longicrure*, may have suffered from insufficient sampling to establish

the complete ranges of its study species [24], there is presently no evidence for the premise that the Wild Coast transition zone could be a distinct marine bioregion, similar to its south-western counterpart. Like the majority of biogeographical studies, many genetic studies show that it is a region in which the ranges of regional sister lineages overlap [8, 45, 46]. However, unlike these other species, there is no evidence that the different species of *Hymenosoma* occur in the same estuaries. All estuaries previously sampled north of the Wild Coast were inhabited by *H. projectum*, which created the impression that *H. longicrure* is absent from the subtropical region. Lack of habitat sharing is most likely a consequence of abbreviated larval development [47] resulting in too few migrants arriving in an estuary at the same time to establish themselves, or too few to be detectable with moderate sampling effort.

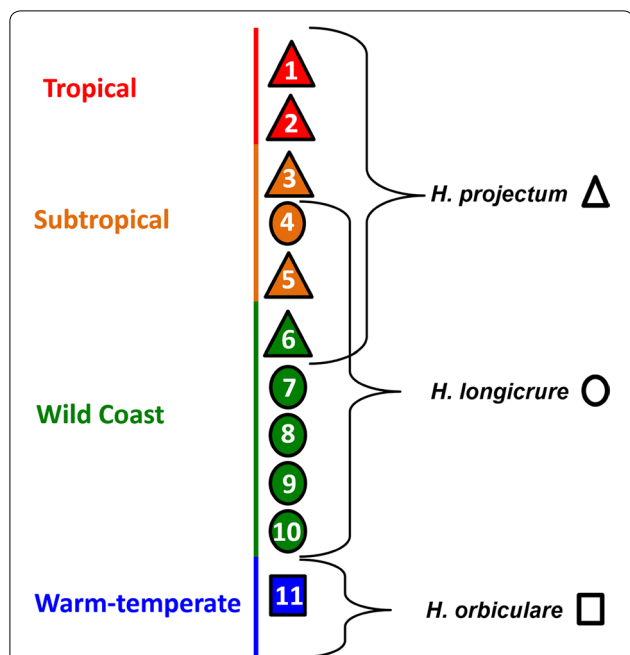


Fig. 3 A diagram depicting the ranges of three species of *Hymenosoma* along the eastern coastline of South Africa. Each marine bioregion is represented by a specific colour, and each species is represented by a specific shape. The brackets show the species' ranges

The identification of unique marine biogeographical regions that may harbour endemic species or populations is essential for the sustainable management of coastal resources. For example, when a widespread marine species is primarily exploited in one of the bioregions in which it occurs, there is a considerable risk of overexploiting a locally adapted population or cryptic species [20, 48]. Because of this, networks of marine protected areas can only be effective if they encompass all of a region's marine biogeographic provinces [3, 20, 49, 50]. The Wild Coast has two large marine protected areas in the north, Pondoland (near site 6) and Dwesa-Cwebe (near site 9), as well as some smaller reserves in the south [51]. These reserves play an important role in preserving the high biodiversity of this transitional zone, as they essentially protect faunal elements from several marine bioregions.

The fauna of the Wild Coast remains poorly studied, and virtually nothing is known about the biology of most of its estuaries. For example, a review of research conducted on South African estuaries [52] listed no biological or ecological information for 73% of the 84 estuaries between the Great Kei and the Mtamvuna Estuary south of Port Edward (Fig. 1). Comprehensive surveys aimed at documenting the region's fauna are urgently needed. This issue is particularly pressing

because of the rapid increase in infrastructure developments in this region [53], including the construction of a coastal highway [54] that will make remote areas of the Wild Coast more accessible. This may facilitate the overexploitation of coastal resources, which is already a major problem along much of South Africa's coastline [55–60]. In addition, even though the present study rejected the idea that *Hymenosoma longicrure* is endemic to this region, it cannot be ruled out that the Wild Coast harbours endemic species. Several endangered or critically endangered species that occur in just a handful of estuaries have been recorded in the well-studied temperate coastal regions of South Africa [61–65], and it is possible that the Wild Coast also has species or genetically distinct populations with very small ranges that have not yet been documented.

Authors' contributions

PRT conceived the research and collected the samples. CMJ and JO generated the genetic data. CMJ, JO and AE-K analysed the data and prepared the figures. CMJ and PRT wrote the paper, with contributions from JO and AE-K. All authors read and approved the final manuscript.

Acknowledgements

We are grateful to Yolanda Qhaji, Isabelle Papadopoulos, Tiru Golla and Sophie Bader for their contributions.

Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The DNA sequences generated for this study have been submitted to the GenBank repository (accession numbers MH325652–MH325882).

Consent for publication

The authors declare that they consent to publish in this journal.

Ethics approval and consent to participate

Sampling was conducted under permit RES2016/70 issued by the Department of Agriculture, Forestry and Fisheries, Republic of South Africa.

Funding

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. CMJ and JO are grateful for bursary support from the University of Johannesburg and the NRF.

Publisher's Note

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Received: 14 February 2018 Accepted: 8 May 2018

Published online: 14 May 2018

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