

Factors affecting seaweed biogeographical and ecological trends along the Namibian coast

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Key words: Namibia, biogeography, sand

Abstract

Namibia forms the northern part of the Benguela marine province in south-western Africa. A splitting of the province into two sub-provinces has been proposed on zoogeographical evidence. This split is the result of decreasing species diversity in the northern regions, and is therefore not a taxonomic division. A number of factors have been found to affect seaweed biogeography on the Namibian coast, e.g. temperature factors, habitat availability and heterogeneity, sand inundation, etc. These factors also have an effect on the local occurrence and abundance of certain species. Biomass sampling quadrats were taken at regular intervals up the shore and the species composition determined. Southern Namibia is separated from northern and central Namibia, due to the dominance of different species. Southern and northern Namibia had a greater horizontal spread on the primary axis of the DCA analysis, reflecting their greater habitat availability and heterogeneity. The shores of central Namibia, in contrast, exhibit minimal variation between shores. The difference between southern and central Namibia is an ecological shift brought about by an increase in temperature in the northern regions and a relatively high degree of sand inundation. The latter has resulted in the dominance of sand-tolerant species. As a result, the sub-province is an ecological entity rather than a floristic one.

Introduction

Namibia comprises the northern half of the Benguela marine province (Engledow *et al.*, 1992; Bolton & Anderson, 1997), which stretches from Moçamêdes (southern Angola, 15° 10' S) to Cape Agulhas (southern-most tip of Africa). This region has also been referred to as the south-western African marine province (Lawson *et al.*, 1990; Lüning, 1990; Field & Griffiths, 1991), or as the 'West Cape' by Hommersand (1986). Stephenson (1948), who looked at the distribution of 318 common intertidal species (a third of these species being algae) around the South African coast, referred to this region as the cold temperate west coast marine province. Emanuel *et al.* (1992) proposed splitting the Benguela province into two distinct biogeographical units based on the results of

a zoogeographical multivariate analysis of invertebrate species presence/absence data. They separated a cool temperate southwest coast (Namaqua province) from a cool temperate northwest coast (Namib province), with Lüderitz marking the border between these two provinces. A similar pattern was observed by Engledow *et al.* (1992), using similar species presence/absence data for seaweeds, but the interpretation of the results differed. The separation of central and northern Namibia from the rest of the west coast was largely due to a decrease in species numbers in these regions and not a floristic change. The Benguela marine province may be divided up as follows:

- (1) a southern coast transitional region (False Bay – Cape Agulhas), between the Benguela and Agulhas marine provinces;

- (2) a characteristic ‘cool’ water adapted south-western coast region (southern Namibia – southwestern Cape); which may be further split into two sub-provinces in the future, but the evidence at this stage is not conclusive; and
- (3) a depauperate ‘warm’ water adapted north-west coast region (northern Namibia – central Namibia).

Here, we take a closer look at the biogeographical trends on the Namibian coast and the factors responsible for them. Not only are broad scale factors such as sea surface temperature important for observed distribution patterns, but also smaller scale or local factors e.g. sand inundation, habitat availability and heterogeneity. These factors may also have an effect on which species become dominant.

Methods

The data used in this analysis comprise seaweed biomass data collected in spring 1990 and autumn

1992. A total of seventeen sites was chosen in southern (SNAM), central (CNAM) and northern (NNAM) Namibia (Fig.1); nine of which were sampled over two seasons (i.e. 1990 & 1992; Table 1). Two to three transect lines were located at each site from spring low-water mark to spring high-water mark. All material was removed from 25 cm x 25 cm quadrats at 1 m intervals on each transect, sorted and the biomass of the various species measured. Details of the method of collection are set out in Engledow *et al.* (1992). To establish site relatedness, the average biomass of each species was estimated for each shore. This was done by the summation of the biomass values for each species within all the quadrats within a particular site, divided by the total number of quadrats at that site. The data were then subjected to a detrended correspondence analysis (DCA – Ter Braak, 1991) to reveal site relatedness.

Results

As can be seen from Figure 2, the Namibian shores separate into the three main regions defined. The

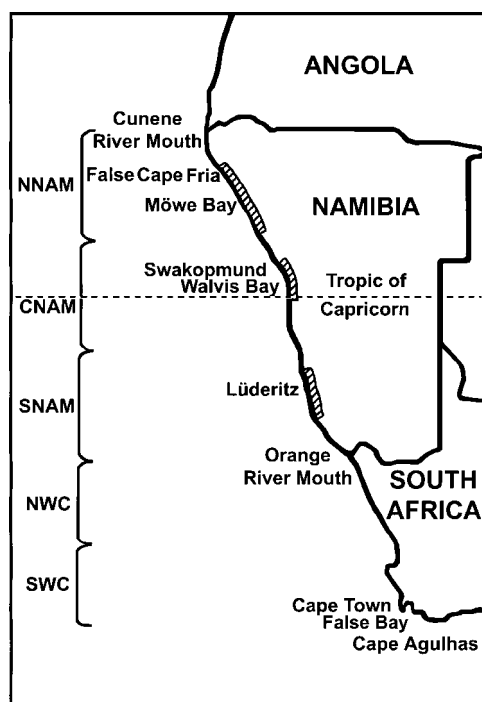


Figure 1. Map of Namibia showing the areas sampled (hatched bands) and regions delineated (See Table 1 for order of sites within the bands).

Table 1. Coding of sites sampled along the Namibian coast in sequence from south to north. Sites in **bold** were sampled in 1990 (Spring) & 1992 (Autumn).

Region	Code	Site
SNAM	ELB	Elizabeth Bay
	GSB	Grossebucht
	KBF	Kleinbogenfels
	ESB	Essy Bay
	DZP	Diaz Point
CNAM	SKI	Shark Island
	L&A	Rocks near Agate Beach
	LGS	Langstrand
	VIN	Vineta Beach
	MY4	Myl 4
NNAM	MY8	Myl 8
	MOW	Möwe Bay
	TOS	Toscanini
	TOR	Torra Bay
	TER	Terrace Bay
	RPT	Rocky Point
	FCF	False Cape Fria

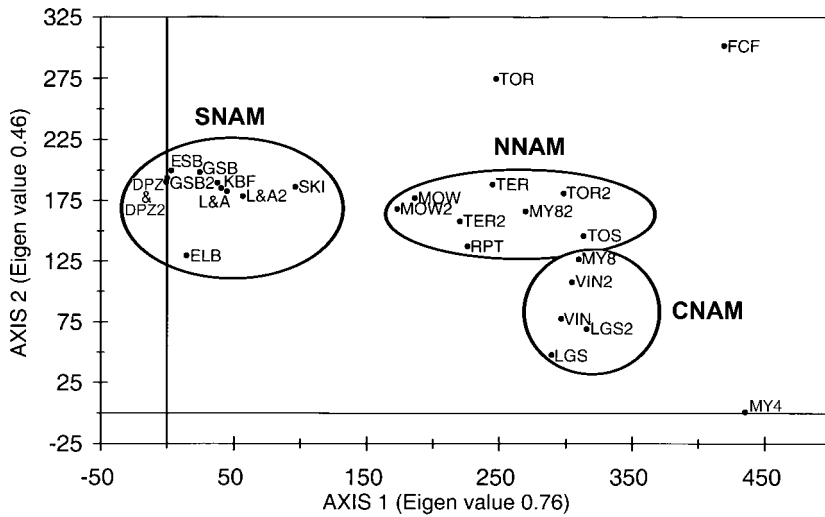


Figure 2. DCA of average biomass for the various sites sampled during 1990 and 1992. (Letter abbreviations followed by the number '2' refer to the samples collected in Autumn 1992, all other samples were collected in Spring 1990).

southern Namibian sites show a close affinity to one another, with the exception of Elizabeth Bay. The southern sites are also clearly separated from the central and northern regions. The sites in southern and northern Namibia are spread horizontally, parallel to Axis 1, showing that they lie on some gradient. The central Namibian sites form an almost cohesive group, with the Myl 8 (1992) site forming part of the Skeleton coast group. The only other outlier is Myl 4, which closely aligns with False Cape Fria on the Axis 1, although they are

separated on Axis 2. The central Namibian sites are closely vertically aligned, showing very little difference with respect to Axis 1, but separate on Axis 2. The Skeleton coast sites are more spread out and diverse. Toscanini on the Skeleton coast has a high degree of similarity with Myl 8 from Swakopmund. Most of the sites that were sampled in both years show very little difference between them, with the exception of Torra Bay. The Skeleton coast is spread out on both axes.

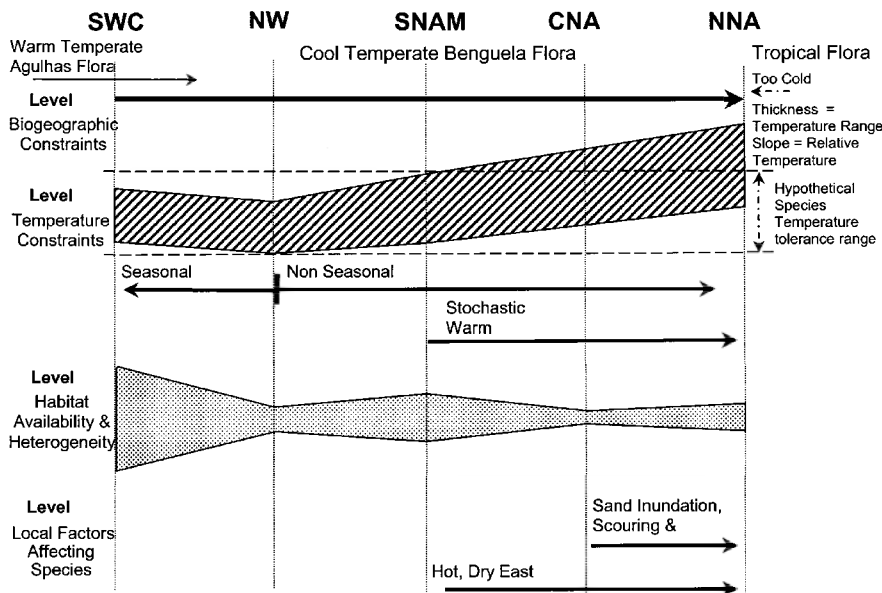


Figure 3. Schematic diagram modeling the major factors affecting seaweed species richness along the Benguela marine province.

Discussion

A number of factors are responsible for the observed decline of species in a south-north direction. Hommersand (1986) attributed this partly to lack of collected material, and this is partially true, but sufficient material has been collected in this study to validate the general trend. Lawson *et al.* (1990) proposed a decrease in wind stress and the related water circulation patterns, but they do not elaborate on how this would affect species richness. A similar pattern of decreasing species richness in a northward direction has been observed on the west coast of South America (Santelices, 1980). This was attributed to the cool influence of the Peru current and temperature increases in the northern reaches due to the southward incursions of subtropical surface water or stochastic water (El Niño). The biogeographical distribution and ecological composition of species may be explained by looking at a hierarchical system of factors or scales. For example, sea surface temperature will have a dominant role to play in determining the presence of many species, while the effects of sand inundation have a more local effect on distribution and dominance. The biogeographical patterns, species diversity and ecological composition observed on the Namibian coast may be explained by the following model based on Engledow *et al.* (1992) (Fig. 3):

Level 1: there is a sudden transition in sea surface temperature between Namibia and Angola. As a result of this rapid transition, few tropical seaweed species can establish in Namibia and *vice versa*, unless they are eurythermal. The temperature changes from 18–21°C (Nature Conservation station at Möwe Bay; Fig.1) in northern Namibia, to 24°C in the north of Moçamêdes in southern Angola based on the summer isotherm (Lawson *et al.*, 1975). This is the result of the confluence of the cool northward flowing Benguela current and the warm southward flowing Angola current. The likelihood of stenothermal species migrating between these two regions is minimal due to the temperature differences. Also, the general sea current direction on the Namibian coast is northerly, which would probably reduce the likelihood of seaweeds migrating south. As a result, the northern boundary of the Namibian seaweed flora is relatively

well defined.

Level 2: Not only is there a temperature discontinuity at the northern extreme, but there is an increase in temperature at Walvis Bay (Bolton, 1986). Mean annual temperatures of the southern regions of the Benguela province are approximately 12–13°C with a range of 11.5–14°C in mean monthly temperature (Bolton, 1986), while in the Walvis Bay area, the annual mean is approximately 16°C with a range of 12–18.4°C (Molloy, 1990). Bolton (1996) hypothesized that a relatively narrow temperature range and a long geological period of prevailing warm temperate conditions would result in high diversity due to the coexistence of both stenothermic and eurythermic species. This change in temperature in central Namibia has probably resulted in halting the spread of more 'cool' water-adapted stenothermal species from venturing further north. This would account for the sudden decline in species richness in the central and northern reaches of Namibia. The shift in temperature range may also influence species dominance. Möwe Bay in Northern Namibia is topographically similar to sites in southern Namibia. The species that dominate this site are however different from those in the south, eg geniculate coralline algae, *Centroceras clavulatum* (C. Agardh) Montagne, *Caulacanthus ustulatus* (Turner) Kützing. These seaweeds are found further south, but are less dominant. They re-emerge as a more dominant component on the warmer South African south coast (the Agulhas marine province).

Unlike the northern reaches of the Benguela marine province, the southern part of the province abuts a warm temperate province (the Agulhas marine province). As a result of warmer temperatures, some species from the Agulhas province are able to survive in southern part of the Benguela marine province for several reasons. The latter area is very heterogeneous with respect to its physical environment, having a diversity of microhabitats or sites (for example, not all areas experience extensive upwelling, e.g. Table Bay, Cape Town). Another reason may be that the species that do live in these southern parts are eurythermal or at their temperature limits, and being near a propagule source (*viz* False Bay, which has a diverse flora due to its wide

temperature gradient) are able to recolonize an area if it becomes locally extinct.

The Namibian coast is subject to upwelling of cool central water, but, unlike the southern part of the flora, it is non-seasonal (Shannon, 1985). This is particularly prevalent in Lüderitz, and, to a lesser extent, further north. The seasonal temperature fluctuations are therefore more defined in the southern reaches. The coastal waters also receive counter-current tongues of warm water from the Angolan current, as well as warm water events caused by the El Niño phenomenon. These may increase the sea surface temperature up to 21°C, while parts of Lüderitz lagoon may reach temperatures of 28°C for periods of one to three weeks. These warm water events may serve as a limiting factor to the spread or establishment of various algae that could potentially occur here. A similar pattern has been noticed on the temperate coast of Pacific South America (Santelices, 1980). The Namibian coast is a less stable situation than that found on the west coast of South Africa, which has a much narrower temperature range and seasonal variation (Bolton, 1986). As a result, seaweeds along this coast are exposed to cool water for most of the year, with occasional warm water events that are tropical in nature. The sea temperature is therefore generally too cold to allow the establishment/survival of tropical species and occasionally too warm for relatively 'stenothermal' warm temperate species, thus limiting the geographical spread of South African west coast and Angolan species.

Level 3: There is a decrease in habitat heterogeneity on a micro and macro scale as one moves northwards. Lüderitz, in southern Namibia, comprises a lagoon, a number of bays, numerous inlets and extensive rocky outcrops ranging from sheltered to extremely exposed. As one moves north of Lüderitz, there is a tailing off of the above, and the coast becomes relatively straight with Sandwich Harbour and Walvis Bay being the only inlets in the central reaches of the country (Branch & Griffiths, 1988). The Skeleton coast consists of long sandy beaches with small rocky outcrops, which are often completely submerged during neap tides. There are, however, a few relatively big rocky

outcrops that are not completely covered by spring high water eg Mōwe Bay, Rocky Point, False Cape Fria and Cape Fria. As a result, the central and northern parts of Namibia are exposed to severe wave action with very few or no sheltered habitats. Likewise, on a micro-scale, there is a plethora of habitats in the south as opposed to the north. The rocky outcrops in southern Namibia usually extend above the spring high water mark and are more diverse with respect to texture, type, morphology and aspect; having numerous rock pools (at all tidal levels), gullies of various dimensions, rocks of various sizes, etc. This diversity is present, to a lesser extent, further north. Thus there are a greater variety of habitats available in the south, allowing for the establishment of a wider range of species.

The above argument may also be used to explain the 'difference' between Bolton & Anderson's (1997) sub-provinces, viz. Namaqua and Southwestern Cape. The latter region, as a percentage of the total coastline, has greater habitat heterogeneity and substrate availability than the former, which may give rise to the observed greater species richness in the south. As mentioned earlier, however, this species difference may not be as pronounced as it appears, even though the drop in species number in the northwestern Cape is probably a real one. Southern Namibia is reasonably habitat heterogeneous and it has a relatively substantial rocky shoreline (although not as much as southwestern Cape). Another component which has not been considered is the offshore islands of southern Namibia, which represent further habitat heterogeneity and which have not been extensively researched (with respect to seaweeds or intertidal communities).

There is not only a decrease in habitat heterogeneity with a decrease in latitude, but also a decrease in habitat availability. In the central and northern regions of Namibia, the rocky outcrops are small, few and separated by long expanses of sandy beaches. The rocky shores would therefore act as small islands, and the sand a barrier to dispersal, ie not a suitable substrate for the attachment of seaweeds.

Level 4: Other local factors may also affect sea-

weed distribution. Sand/silt inundation of rocky shores is more prevalent in the central and northern reaches of the Namibian coast. One would expect to find sand-tolerant species (eg *Mazzaella capensis* (J.Agardh) Fredericq – Bolton & Joska, 1993) and the exclusion of sand-intolerant species (*Aeodes orbitosa* (Suhr) Schmitz – Bolton & Levitt, 1992). *Mazzaella capensis* is able to ‘resprout’ from its crustose base after a sand inundation event, while *Aeodes orbitosa* has no such persisting structure. Sand inundation, together with increased temperature conditions and possible related increases in herbivory, could account for the predominance of turf-forming seaweeds (eg *Chylocladia capensis* Harvey, *Ophidocladus simplicusculus* (Crouan & Crouan) Falkenberg in Engler & Prantl, *Cladophora* spp., *Caulacanthus ustulatus* (Turner) Kützing, *Polysiphonia* spp., *Tayloriella tenebrosa* (Harvey) Kylin) in the central and northern parts of the coast.

The potential exists for mass destruction of seaweeds and other intertidal organisms during east wind conditions on the coast of Namibia. This wind is hot and dry, and blows off the desert onto the rocky shore. If these winds coincide with low tide, they may have potentially devastating effects on the intertidal organisms. The bleaching of many intertidal seaweeds has been noted during such an event in Swakopmund (central Namibia). The severe desiccating effect of a similar wind in southern California was noted by Seapy & Littler (1982). The effect of this wind may have a profound effect on the intertidal diversity and species richness in that it may cause ‘local extinction’ of species. This, coupled with the fact that potential propagule sources, *viz.* close unaffected rocky shore, are relatively rare in the central and northern Namibian regions, means that recolonization of these shores is severely restricted.

The reduced species richness of the central and northern reaches of Namibia can be attributed to the above. Temperature in conjunction with habitat (including wave action) and propagule source would set the range of species that could potentially survive in the given region. This range is further influenced by the species ability to tolerate events such as sand-inundation, warm water intrusion

and low tide east wind events.

As was seen in Figure 2, southern Namibia is separated from northern and central Namibia. This is due to the dominance of different species in these regions. As was described above, there is a rise in temperature in the central region of Namibia, which would account for some of the observed shift. Also, southern and central Namibia were both found to be spread out on the primary axis. This may be explained by the increased habitat availability and heterogeneity found in these regions; while central Namibia lies virtually on one line on the primary axis and separated on the secondary axis. The latter is due to the fact that the species composition on these shores is very similar, and only the biomass values for the various species vary, giving the observed dispersion on the secondary axis. Central and northern Namibian sites are however more closely aligned to one another than those of southern Namibia. The Namibian coast may thus be divided into two main areas:

- (1) a southern region, which is similar to communities of South African west coast shores; and
- (2) a central and northern region.

The latter region has a predominance of turf-forming, ‘resprouting’ (those species with a persistent crustose base) and opportunistic algal species. These two regions represent an ecological shift and not a floristic change driven by the factors outlined above, in particular: temperature, degree of sand inundation, and possibly wave exposure. A number of species are excluded from the central and northern regions of Namibia on the basis of the rise in temperature. Other species are then able to become dominant because:

- (1) there is the absence of dominant/late successional species further south;
- (2) they are better adapted to the increased temperature; and or
- (3) they are able to cope with a moderate to high degree of sand inundation on most shores.

The changes between the three regions and their various sites show a species response to the prevailing conditions. As a result, a number of species may be implicated as being environmental

indicators for particular conditions along this coastline.

Acknowledgements

The authors would like to thank the National Research Foundation, Department of Environment and Tourism and the University of Cape Town for support. We would also like to thank the Namibian department of Sea Fisheries for their cooperation with respect to permits and use of facilities in Lüderitz and Swakopmund.

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