Ocean currents shape the genetic structure of the kelp *Laminaria pallida* in southwestern Africa

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Abstract

Aim: Drivers of extant population genetic structure include past climate-driven range shifts and vicariant events, as well as gene flow mediated by dispersal and habitat continuity. Their integration as alternative or complementary drivers is however often missing or incomplete, potentially overlooking relevant processes and time scales. Here we ask whether it is the imprint of past range shifts or habitat connectivity driven by oceanographic transport that best explain genetic structure in a poorly understood model, a forest-forming African kelp.

Location: Southwestern coast of Africa (Benguela current region).

Taxon: *Laminaria pallida.*

Methods: We estimated genetic variability along the species distributional range using 14 microsatellite markers. This was compared to estimates of past range shifts derived from species distribution modelling for the Last Glacial Maximum (LGM), the mid-Holocene (MH) and the present, and estimates of habitat connectivity derived from oceanographic biophysical modelling.

Results: The species is structured in two well-defined clusters, a southern cluster with much richer (allelic richness A: 10.40±0.33) and unique (private alleles PA: 56.69±4.05) genetic diversity, and a northern cluster (A: 4.75±0.17; PA: 6.70±1.45). These clusters matched well-known biogeographic regions and their transition coincided with a dispersal barrier formed by upwelled offshore transport. No major climate-driven range shifts or vicariant events were hindcasted along the present range, suggesting population stability from the LGM to the present.

Main conclusions: Habitat connectivity, rather than past range shifts, explains the extant population structure. Future environmental requirements of the species along the Benguela upwelling system are projected to persist or even intensify, likely preserving the observed

genetic patterns for the years to come. Yet, the differentiation and endemicity between genetic groups, and the inferred isolation structured by the regional oceanography, implies high conservation value for genetic biodiversity, and even more if considering the multiple ecological, social, and economic services provided by kelp forests.

Introduction

Marine species exhibit considerable variation in their dispersal potential, ranging from near panmixia to highly structured meta-populations. Sessile organisms lacking long-lived dispersive stages (e.g., pelagic larvae) tend to exhibit relatively short dispersal kernels and considerable population genetic structure across their ranges. This often reflects the imprints left from past events, such as vicariance and range shifts experienced throughout glacial-interglacial cycles (Assis et al., 2016, 2018; Maggs et al., 2008; Phair et al., 2019; Song et al., 2021; Toms et al., 2014). In particular, endemic lineages often coincide where species persisted during both cold and warm climatic extremes (i.e., within climatic refugia), while more recently colonized areas tend to show homogeneous populations with reduced diversity owing to genetic bottlenecks resulting from founder effects. Dispersal can further influence population genetic structure, maintaining or diluting the imprints of past events (Alberto et al., 2011; Assis et al., 2018; Buonomo et al., 2016; Lourenço et al., 2017; Silva et al., 2014). While main oceanographic processes (e.g., upwelling) can help preserve genetic differentiation (Henriques et al., 2014, 2016), periodic events characterized by strong oceanographic currents or upwelling disruptions can promote long distance connectivity and gene flow, even for low dispersal species (Batista et al., 2018; Gunawickrama et al., 2020). Disentangling the potential drivers of population genetic structure has much biogeographical and evolutionary relevance (Assis et al., 2018), as well as conservation and management implications (Mertens et al., 2018; Nepper-Davidsen et al., 2021), but their integration is often neglected, potentially leading to conclusions biased towards the particular process analysed, and overlooking their relative mutual influence.

Southwestern Africa is an ideal region to explore the potential drivers of population genetic structure, owing to its linear coastline with sharp environmental gradients over short geographic distances. The region is dominated by upwelling from the northward-flowing Benguela current, which results in one of the world's most important eastern boundary

upwelling systems (Kämpf & Chapman, 2016). This sustains the very productive Benguela province (Spalding et al., 2007), which includes major sub-Saharan kelp forest ecosystems (Rothman, Bolton, et al., 2017). To the north, this region is delimited by the Angolan ecoregion, where a sharp transition to tropical conditions and communities occurs (Anderson et al., 2012; Spalding et al., 2007). Drivers of marine population structure along southwestern Africa remain insufficiently documented, but high levels of intraspecific genetic variation have been reported for several species of fish and invertebrates. Genetic breaks can vary considerably (Teske et al., 2011; Von der Heyden et al., 2013), but some congruence has been found, with species displaying distinct lineages (and even sibling species) within well-defined regions (Evans et al., 2004; Henriques et al., 2014, 2016; Reid et al., 2016; Schulze et al., 2020; Teske et al., 2006). Studies have attributed the observed patterns to life-history traits and contemporary selection (Phair et al., 2019; Teske et al., 2019), paleoceanographic sea-level changes (down to -120 m during the Last Glacial Maximum, LGM, ca. 20,000 years ago) and associated coastline displacements (Toms et al., 2014), as well as oceanographic transport and its inherent processes (Gunawickrama et al., 2020; Henriques et al., 2012, 2014, 2016; Schulze et al., 2020). In particular, the strong upwelling front centred off Lüderitz (approx. 26°S latitude) promotes powerful offshore advection of Benguela current and represents a permanent dispersal barrier for numerous marine species inhabiting the region (Gunawickrama et al., 2020; Henriques et al., 2012, 2014, 2016; Schulze et al., 2020) and is a general marine biogeographic break (Spalding et al. 2017). The impact of past climate-driven range shifts has not been recognized as a major driver of genetic structure in southwestern Africa (Nielsen et al., 2021), contrasting to what has been widely suggested in the Northeast Atlantic and the Southwest and Northwest Pacific (Assis et al., 2016, 2018; Fraser et al., 2009; Neiva et al., 2018; Song et al., 2021). Glacial advances could have not impacted coastal distributions, as the southern continental limit of Africa lies at ca. 35° latitude, well beyond the reach of glacial ice (Peltier, 2004). However, paleo species distribution modelling (SDM) exploring climate-driven range shifts are limited in the region

(Robinson et al., 2017), and one of the few attempts there actually show the potential for past range shifts (Nielsen et al., 2021), likely related to the intensification of the Benguela upwelling system and/or the weakening of the warmer Agulhas current (Hutson, 1980; Romero et al., 2003; Thackeray, 2016).

Despite the efforts over the past decades, knowledge gaps persist for southwestern Africa. Phylogeographic research has been mostly performed with mtDNA markers, typically lacking resolution and prone to selection (Teske et al., 2018), remains heavily biased towards fish and invertebrate species with high dispersal potential, and largely overlooks the west coast Benguela upwelling region, despite its high levels of regional endemism (Teske et al., 2011). The present study addresses some of these gaps, by asking whether genetic structure of the forest-forming African kelp *Laminaria pallida* is explained by past climate-driven range shifts and shoreline displacements associated with sea level changes, and/or habitat connectivity mediated by oceanographic transport. The species represents an ideal model to investigate the subject, owing to the limited spore dispersal of *Laminaria* species, which allows retention of the imprints of past changes, while local populations can saturate available rocky shore habitats and promote density barriers, further buffering the homogenizing effect of gene-flow. Additionally, long-range dispersal by rafting of *Laminaria* fronds or entangled in other floating seaweed is possible (Clarkin et al., 2012), extending dispersal distances and distributional ranges across biogeographic regions (Assis et al., 2018). These traits and processes have been reported for kelp elsewhere (Assis et al., 2016, 2018; Fraser et al., 2009; Neiva et al., 2018; Song et al., 2021), but never were never addressed in southwestern Africa, notwithstanding the regional economic and ecological importance of kelps, including the multiple ecosystem services provided (Blamey & Bolton, 2018).

We compared the species' genetic variability inferred from polymorphic microsatellite markers with estimates of past range shifts and habitat connectivity derived from distribution and biophysical modelling. We hypothesize that (1) climate changes associated with the

intensification of the Benguela upwelling system and the weakening of the Agulhas current (Hutson, 1980; Romero et al., 2003; Thackeray, 2016), coupled with coastline displacements associated with sea level changes (Toms et al., 2014), produced past range shifts and shaped the extant genetic structure of *Laminaria pallida*. In this process, (2) the classic paradigm of low latitude refugia (Assis et al., 2016, 2018; Maggs et al., 2008) is not hypothesized, since there is no evidence for the direct impact of glacial ice in the higher latitudes of southwestern Africa. Additionally, (3) connectivity between rocky habitats shaped by the major oceanographic patterns of the Benguela current, promoting asymmetrical long-distance dispersal (Stenevik et al., 2008) and semi-permanent upwelling conditions, are further hypothesized to have driven the genetic structure of the species. In particular, the upwelling front centered off Lüderitz should coincide with the genetic discontinuities of *L. pallida*, as inferred for numerous species there (Gunawickrama et al., 2020; Henriques et al., 2012, 2014, 2016; Schulze et al., 2020), while the fewer and patchier rocky reefs in the northern range (Fig. 1) played a role in structuring diversity patterns. We contribute to a broader understanding of the drivers of marine phylogeography along this unique region, particularly overlooked for species with limited dispersal. Moreover, describing the location and drivers of endemic genetic lineages of kelps is timely, as their global persistence is threatened by projected climate changes (Arafeh-Dalmau et al., 2020; Assis, Araújo, et al., 2017).

Methods

Study area and focal species

The study was performed along the full continental distributional range of *Laminaria pallida*, which covers the Benguela upwelling region, from ca. 100 km east of Cape Town to near the Kunene River in northern Namibia (Bolton & Stegenga, 2002). Some temperate islands where the species is reported to occur (Assis et al., 2020) were not included in the analyses. Due to its geographically variable morphology, the species was previously considered two species: the solid-stiped form *L. pallida* and the hollow-stiped form *L. schinzii* (Rothman, Bolton, et al., 2017; Rothman, Mattio, et al., 2017). However, these are now considered conspecific, with the solid-stiped form found at its southern subtidal distribution. Northward, the species becomes progressively abundant inshore, with its stipes becoming gradually hollower. The species represents a major rocky reef ecosystem in the Benguela upwelling region, dominating the lower intertidal and shallow depths (Rothman, Bolton, et al., 2017).

Genetic diversity and structure

Laminaria pallida populations were sampled from 20 sites between Rocky Point (Northern Namibia, -19.0º Lat.) and Stanford's Cove (Western Cape, South Africa, -34.5º Lat.; Table 1; Fig. 1). At each site, tissue samples were collected haphazardly in the low-intertidal zone by walking along the entire accessible population to collect up to 30 individuals, ensuring at least one meter between consecutive algae, or, when populations were very small and concentrated, that different individuals were collected. Six additional samples (sites 1-5; Table 1) were collected as drift material, primarily in northern Namibia, to investigate their putative origin and potential evidence for long-distance drift-mediated dispersal. Samples were individually stored and dehydrated in silica-gel crystals until DNA extraction.

Genomic DNA was extracted using the Nucleospin Multi-96 plant kit (Macherey-Nagel Duren, Germany), according to the manufacturer's protocol. Fourteen microsatellite loci were amplified to generate multi-locus genotypes in all individuals, following previously developed methods for congeneric species *L. ochroleuca* (Coelho et al., 2014) and *L. digitata* (Billot et al., 1998). Polymerase chain reactions (PCRs) were performed in 15 µL total volume containing 1× GoTaq Flexi buffer, 1.5–2.0 mM $MgCl_2$, 125 µM each dNTP, 0.2-0.5 µM of labelled (FAM, NED, HEX, ROX) forward and 0.5 µM simple reverse primers, 0.5-1 U GoTaq Flexi DNA Polymerase (Promega), and 1 µL of 1:10 or 1:100 diluted DNA template. An initial denaturation step (94 ºC, 5 min) was followed by 30 cycles of 94 ºC for 30 s, a primer-specific annealing temperature (T_a) for 30 s and 72 ºC for 45 s, ending with a final extension step at 72 ºC for 10 min (see Table S1 for primer names, sequences, and a summary of amplification details). Amplified fragments were separated using an ABI PRISM capillary sequencer (Applied Biosystems, CCMAR, Portugal). Alleles were manually scored in STRand (Toonen & Hughes, 2001) independently by JN, LG and HM using the 500 LIZ™ size standard (Applied Biosystems). These data were tested for null alleles and neutrality with Microchecker (Van Oosterhout et al., 2004) and Popgene (Yeh & Boyle, 1997), respectively. See data availability section for multi-locus genotypes per site.

Genetic diversity was estimated as standardized allelic richness, Nei's gene diversity and number of private alleles using R software (R Development Core Team, 2021) with the package diversity (Keenan et al., 2013). The same statistics were computed for the most differentiated genetic clusters found (described in results below). Genetic structure was inferred with Structure (Pritchard et al., 2000) without any prior population assignments. A range of assumed clusters (K, from 1 to 10) was run 25 times using a burn-in of 1,000,000 iterations and a run-length of 1,000,000 iterations. The ΔK criterion (Evanno et al., 2005) inferred the likely number K clusters. Pairwise genetic differentiation between clusters was determined as Jost's D (Whitlock, 2011) with the R package diveRsity. Hierarchical analysis

of molecular variance (AMOVA) performed with Genodive (Meirmans & Van Tienderen, 2004) tested the clustering assignments of Structure. This was based on allele frequency information with 10,000 permutations, with variance components extracted between sites, within genetic clusters, and between genetic clusters.

Species distribution models to infer past range shifts

Range shifts from the LGM to the present were inferred with species distribution modelling using Boosted Regression Trees (BRT) and Adaptive Boosting (AdaBoost), two machine-learning algorithms known for high predictive performances and the ability to fit complex relationships and interactions (Elith et al., 2008). The algorithms modelled occurrence records (presence / absence) against biologically meaningful climatic predictors for marine forest species, while avoiding overfitting (i.e., complex fit of random noise) through monotonic responses (Hofner et al., 2011) and optimized parameterization procedures (Assis, Araújo, et al., 2017; Elith et al., 2008).

Climatic predictors for present-day conditions (climatology of 2000-2017), the warmer mid-Holocene (MH; ca. 6,000 years ago) and the Last Glacial Maximum (LGM; ca. 21,000 years ago) were downloaded from Bio-ORACLE (Assis, Tyberghein, et al., 2017; see data availability section); namely, nutrients (as nitrate and phosphate), salinity and ocean temperatures (maximum and minimum). These data considered the weighting of different Atmospheric-Ocean General Circulation Models (AOGCM; Assis, Tyberghein, et al., 2017) as well as the potential -120 m sea level change during the LGM (Assis et al., 2016, 2018; Peltier, 2004). Prior to modelling, Pearson's correlation coefficient was inferred between all pairs of predictors. Georeferenced presence records for the whole species distribution were compiled from a fine-tuned dataset of marine forests (Assis et al., 2020), while pseudo-absences were generated randomly to better calibrate models and isolate highly contributive

variables (Cerasoli et al., 2017). To account for sampling bias and restrict modelling to the actual extent of the species domain, pseudo-absences were chosen from a kernel probability surface produced with the presence records and a spatial grid with the same resolution as the climate data (Assis, Araújo, et al., 2017). To reduce the potential effect of spatial autocorrelation, the correlation of climatic predictors within the range of presence records was determined as a function of increasing marine distances using Mantel tests under 1×10^4 permutations (Boavida et al., 2016). The minimum non-correlated distance identified was used to trim records and remove overlapping surplus information.

Over-fitting and generalization were controlled by tuning BRT and AdaBoost hyperparameters (Assis, Araújo, et al., 2017; Fragkopoulou et al., 2021; Martins et al., 2021 for details) and by forcing monotonicity constrained responses (positive for salinity, nutrients and minimum temperature, and negative for maximum temperature; Hofner et al., 2011). A 10-fold cross-validation framework using independent latitudinal bands was implemented in this process (Assis, Araújo, et al., 2017). Models were produced with all combinations of BRT and AdaBoost parameters, fitting data interactively with one latitudinal band withheld at a time. The performance of each set of parameters was evaluated with the area under the curve of the receiver operating characteristic (AUC).

Final predictive models fitting occurrence records and predictor variables, and tuned with the optimal parameters (i.e., those retrieving higher average AUC values in cross-validation) were transferred to the climatologies of the LGM, MH and present to estimate the potential distribution of L. pallida through time. The predicted surfaces were reclassified to binomial surfaces representing presence and absences with a threshold maximizing sensitivity and specificity (true positive and negative rates, respectively; Allouche et al., 2006). Final performance scores were reported with AUC, sensitivity, and specificity. The ecological relevance of models was further assessed by determining the relative contribution of each climate predictor to the models (Elith et al., 2008), and by estimating physiological limits

points extracted from each climatic predictors, within the range of values found in the regions providing suitable conditions for the species, as inferred from the binomial predictive surfaces (Assis, Araújo, et al., 2017).

Biophysical modelling

Biophysical modelling was implemented following the approach of previous studies (Assis et al., 2021; Buonomo et al., 2016; Nicastro et al., 2019). This used data from the Hybrid Coordinate Ocean Model (HYCOM), a product providing daily current velocity fields at a resolution of 0.08° (approx. 6–9 km), and able to resolve complex eddies, meandering currents, fronts, and filaments (Chassignet et al., 2007), i.e., key mesoscale processes to simulate passively dispersing propagules (Assis et al., 2021).

The model comprised ~2250 km of coastlines, slightly exceeding the range of the species. A high-resolution polygon defining global landmasses (Haklay & Weber, 2008) limited the simulation. A rocky bottom cartography layer (Harris, 2012) was used to define source/sink sites along the coastline, 1 km apart, from which individual particles were released daily. Particles were allowed to passively drift for up to 30 days until they eventually reached the shore or were lost offshore. This period was considered extreme for long-lived rafts, in line with previous estimates for brown algae, including the closely related species *L. ochroleuca* (Assis et al., 2018; Monteiro et al., 2016). The geographic position of individual particles was determined hourly with bilinear interpolation over the velocity fields. Particle trajectories were aggregated as pairwise matrices representing the probability of connectivity between source/sink sites, by dividing the number of events a particle released from site *i* reached site *j*, by the total amount of particles released from site *i*. The potential inter-annual variability in ocean flow was assessed by running simulations individually for a period of 10 years (2008 to 2017), and by producing an averaged asymmetrical connectivity matrix.

The connectivity between the sites sampled for genetics was inferred by considering stepping-stone estimates of probability of connectivity (Assis et al., 2021; Buonomo et al., 2016). For this approach, graph theory was implemented, with nodes defined by site locations and edges by the probabilities of connectivity. The Floyd–Warshall's algorithm, minimizing the sum of log-transformed probabilities, estimated the shortest connectivity paths between sites, from which probabilities were determined with a product function. As the actual dispersal period of *L. pallida* is unknown, an estimate was performed by comparing the marginal effect on Akaike information criterion (AIC) between linear models fitting probability of connectivity and genetic differentiation (Jost's D), for the span of propagule durations simulated in the biophysical modelling (i.e., 1 to 30 days). The model retrieving the lowest AIC, i.e., best explaining differentiation, was used as a final estimate of the species' potential dispersal period. Finally, two competing linear regression models were developed fitting genetic differentiation (Jost's D) against (1) a null model of alongshore marine distances (i.e., isolation by distance model) and (2) a stepping-stone probability of connectivity tunned with the dispersal period previously inferred. The models were compared using adjusted R-square, Pearson's correlation coefficient and Akaike information criteria (AIC).

Species distribution modelling, biophysical modelling and network analyses were performed using the R packages dismo, gbm, parallel, sdm SDMTools igraph, raster and vegan.

Results

Genetic diversity and structure

A total of 451 multi-locus genotypes were produced from the 20 sites sampled (n=442) plus the few drift algae (n=9) from 6 additional sites. Microsatellite polymorphism within the 14-loci dataset varied from 7 to 49 alleles per locus, with a mean of 16.64 alleles per locus. These data showed consistent evidence of null alleles in three loci (Ld158, Lo454-18 and Lo4-13; Table S2) and selection in three loci (Ld158, Lo454-24, Lo4-13; Table S3). To account for the potential effect of null alleles and selection in our results, an additional analysis of structure was performed without the potentially affected loci (i.e., Ld158, Lo454-24, Lo454-18 and Lo4-13). Because this did not change the main results (Fig. S1; Fig. 1), we did not exclude these loci from the analyses.

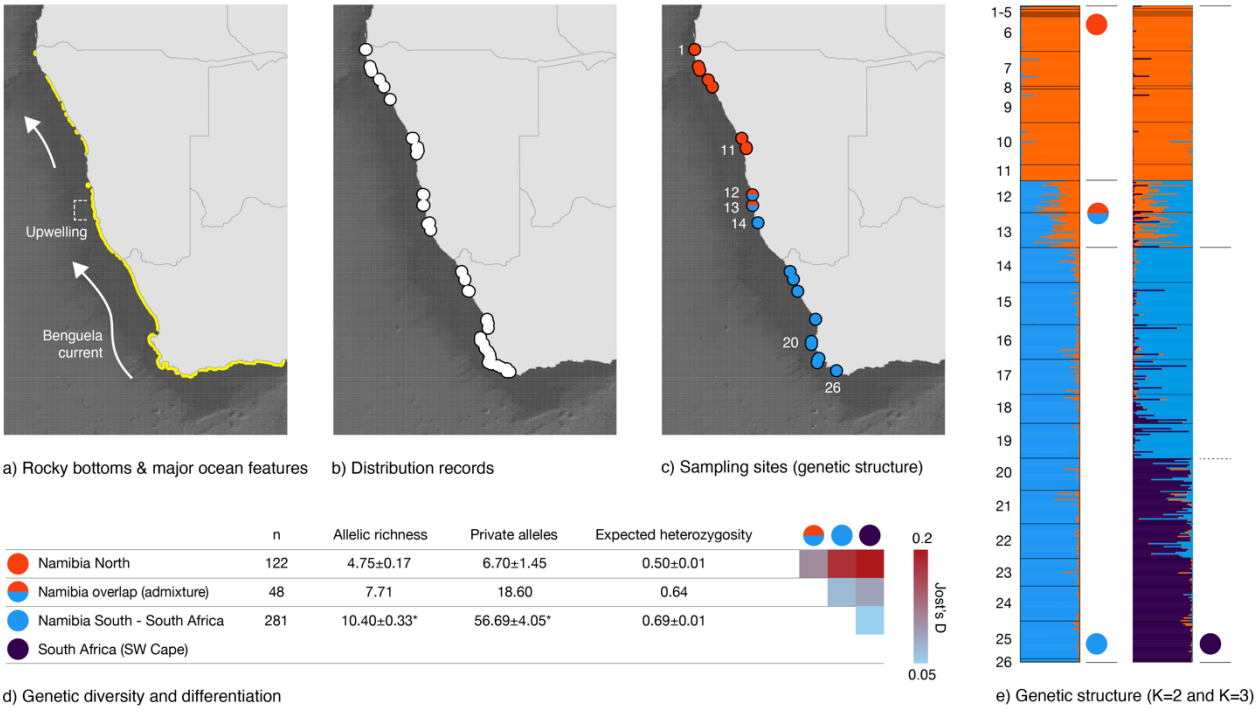
Within sites, standardized allelic richness (A), endemism (PA) and gene diversity (HE) were very variable (Table 1), with A showing a general increasing trend with latitude, with one exception for the southernmost site. In particular, the region comprising the sites from Hondeklip Bay to Jacobs Bay (South Africa; sites 17-22) exhibited the highest intra-population diversity levels, with A up to 7.76±0.15 (Hondeklip, site 17), PA up to 5.75±1.10 (Jacobs Bay, site 22) and HE up to 0.70±0.01 (Doring Bay, site 18). Diversity was much lower at lower latitudes (central and northern Namibia), where A ranged between 2.9 and 3.96±0.09, whereas no PA were observed in 2 out of 5 populations (max. PA 0.43±0.60 in Rocky Point, site 6). The lowest HEs were also found there (Mile 4 and Rocky Point, sites 9 and 6; Table 1).

Table 1. Genetic diversity of *Laminaria pallida* at each site based on 14 microsatellite loci. Code (#), region, site name, coordinates (Latitude and Longitude in decimal degrees), sample type (drift versus attached population), number of individuals (n), allelic richness (A), number of private alleles (PA) and Nei's gene diversity (expected heterozygosity; He). Diversity indices were estimated after standardizing the sample size to 20 individuals per population, where higher.

#	Region	Name	Lat	Lon	Type	n	A	PA	He
1	Namibia North	Bosluis Bay	-17.369	11.757	Drift	2	1.79		0.54
2	Namibia North	Portuguese Lorry	-17.559	11.735	Drift	2	2.07		0.54
3	Namibia North	Shipwreck	-19.140	12.592	Drift	1	1.36		0.19
4	Namibia North	False Cape Fria	-18.485	12.025	Drift	1	1.79		0.33
5	Namibia North	Angra Fria	-18.273	11.958	Drift	1	1.36		0.36
6	Namibia North	Rocky Point	-18.994	12.475	Attached	24	3.83±0.10	0.43±0.60	0.49±0.01
7	Namibia North	Moewe Bay	-19.369	12.705	Attached	24	3.96±0.09	0.15±0.36	0.50±0.01
8	Namibia North	Students Bay	-20.133	13.126	Drift	2	1.86		
9	Namibia North	Mile 4	-22.606	14.515	Attached	23	3.52±0.09		0.48±0.01
10	Namibia North	Henties Bay	-22.122	14.278	Attached	29	3.85±0.12	0.01±0.04	0.51±0.01
11	Namibia North	Swakopmund	-22.672	14.522	Attached	11	2.90		0.49
12	Namibia South	Sylvia Hill	-25.146	14.846	Attached	22	6.44±0.09	2.43±0.83	0.64±0.01
13	Namibia South	Spencer Bay	-25.709	14.847	Attached	24	6.09±0.11	1.28±0.74	0.64
14	Namibia South	Lüderitz	-26.646	15.149	Attached	24	6.22±0.15	2.30±0.59	0.59±0.01
15	South Africa North	Port Nolloth	-29.255	16.866	Attached	29	7.42±0.22	5.04±1.26	0.65±0.01
16	South Africa North	Kleinzee	-29.673	17.044	Attached	24	7.43±0.15	0.34±0.56	0.66±0.02
17	South Africa North	Hondeklip Bay	-30.315	17.27	Attached	24	7.76±0.15	3.01±1.02	0.66±0.01
18	South Africa North	Doring Bay 1	-31.814	18.233	Attached	20	7.21±0.10	3.22±0.44	0.70±0.01
19	South Africa North	Doring Bay 2	-31.814	18.233	Attached	24	7.35±0.16	2.21±0.84	0.67±0.01
20	South Africa Cape	Paternoster	-32.805	17.884	Attached	22	6.56±0.11	3.42±0.88	0.65
21	South Africa Cape	Jacobs Bay 1	-32.967	17.883	Attached	23	6.77±0.18	1.03±0.53	0.67
22	South Africa Cape	Jacobs Bay 2	-32.967	17.883	Attached	24	7.50±0.15	5.75±1.10	0.68
23	South Africa Cape	Mouille Point	-33.898	18.409	Attached	19	4.79±0.30	0.80	0.55±0.01
24	South Africa Cape	Oudekraal	-33.987	18.348	Attached	24	6.53±0.16	2.66±0.95	0.55±0.01
25	South Africa Cape	Kommetjie	-34.142	18.321	Attached	26	6.91±0.20	5.90±1.33	0.60±0.01
26	South Africa Cape	Stanford's Cove	-34.566	19.352	Attached	2	1.93		0.48

The ΔK criterion divided *L. pallida* into 2 main genetic clusters, with a narrow intermediate region of admixture (Fig. 1; Fig. S2): (1) the Namibia North cluster (northern group), including the sites from Bosluis Bay to Swakopmund (sites 1-11) and (2) the Namibia South - South Africa cluster (southern group), including the sites from Lüderitz (14, Namibia South) to

Stanford's Cove (site 26). The contact zone can be considered a third cluster (3), the Namibia overlap, a region of admixture including Sylvia Hill and Spencer Bay (sites 12-13). The southern group was further subdivided into smaller (K=3) subclusters although with weaker support (Fig. S2), but still showing stable compositions and a clear geographic signal (Fig. 1). Subclustering included the sites from Luderitz (site 14) to Doring Baai (site 19), and Paternoster (close to Cape Columbine) to Stanford's Cove (sites 20-26).



a) Rocky bottoms & major ocean features b) Distribution records c) Sampling sites (genetic structure)

	n	Allelic richness	Private alleles	Expected heterozygosity
Namibia North	122	4.75±0.17	6.70±1.45	0.50±0.01
Namibia overlap (admixture)	48	7.71	18.60	0.64
Namibia South - South Africa	281	10.40±0.33*	56.69±4.05*	0.69±0.01
South Africa (SW Cape)				

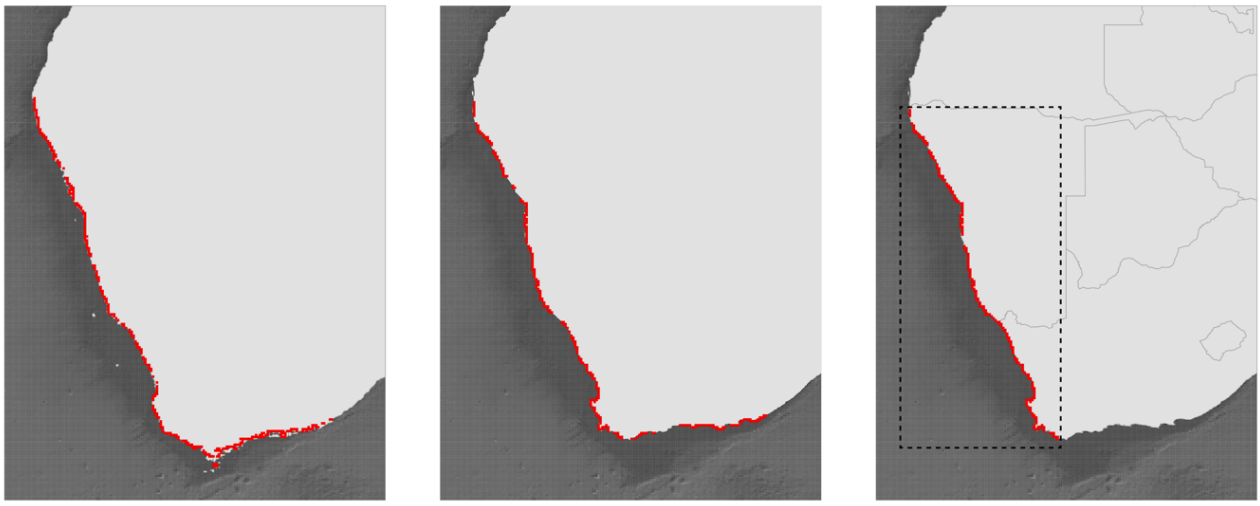
d) Genetic diversity and differentiation e) Genetic structure (K=2 and K=3)

Figure 1. (panel a) Presence of rocky bottoms along the coastline (yellow) and major oceanographic patterns (Benguela current direction and the relative location of Lüderitz upwelling cell; Kämpf & Chapman, 2016), (panel b) records of *L. pallida* occurrence used in SDM and (panel c) sampling locations coloured according to the best supported number of genetic groups (K=2). (Panel d) Genetic diversity per cluster (K=2) as allelic richness, number of private alleles and Nei's gene diversity (expected heterozygosity), standardized for an equal-sized sample of 48 individuals (n). Pairwise genetic differentiation (as Jost's D) between genetic clusters. (Panel e) Genetic structure shown as individual assignments to genetic clusters (K=2 and K=3). Site names and coordinates are listed in Table 1.

371 The analysis of molecular variance (AMOVA) based on Jost's D showed significant
372 differentiation levels within and between genetic clusters (Table S4). Differentiation levels
373 were higher between the Namibia North and both southern sub-clusters (Jost's D > 0.15; Fig.
374 1) and lower between the admixture region (Namibia overlap) and both southern sub-clusters
375 (Jost's D: 0.07 and 0.08; Fig. 1), as well as between both southern sub-clusters (Jost's D:
376 0.06; Fig. 1). Genetic diversity per cluster was significantly higher in Namibia South - South
377 Africa cluster. This displayed more than two-fold allelic richness and nine-fold more private
378 alleles when compared to the Namibia North cluster, and three-fold more private alleles when
379 compared to the admixture region (Namibia overlap). Nei's gene diversity also followed a
380 pattern of higher values in the southern cluster (Fig. 1).

381

382 **Species distribution modelling**



a) Last Glacial Maximum (~20,000 years ago) b) Mid–Holocene (~6,000 years ago) c) Present (climatology 2000–2017)

	AUC (Cross-validation)	AUC (Final)	Sensitivity (Final)	Specificity (Final)	True Skill Statistic
Boosted Regression Trees	0.95±0.05	0.97	0.97	0.93	0.90
Adaptive Boosting	0.96±0.04	0.96	0.97	0.91	0.88
Ensemble of algorithms	-	0.98	1	0.91	0.91

383 d) Species distribution modelling performance

384 Figure 2. Predicted distribution of *L. pallida* for (panel a) the Last Glacial Maximum, (b) the
385 Mid-Holocene and (panel c) the present. Dashed polygon depicts the refugial region
386 providing suitable conditions in the 3 time periods. (panel d) Performance of species

387 distribution modelling assessed with cross-validation and the final models predicting for
388 present-day conditions.

389

390 Distribution models fitting the occurrence records (Fig. S3) and meaningful predictors
391 showed high predictive performance, both when tested with independent data (cross-
392 validation) and with the final prediction developed for present-day conditions (AUCs > 0.95;
393 Sensitivity > 0.97; Specificity > 0.91; Fig. 2). The ensemble of algorithms accurately predicted
394 the distribution of *L. pallida* (AUC: 0.98, Sensitivity = 1; Fig. 2). The most important predictors
395 explaining the distribution of *L. pallida* (considering the region and resolution where the
396 models were fitted) were maximum and minimum temperatures, as well as nutrients (relative
397 contributions > 5%). Salinity had no contribution to the models (Fig. S4). These inferences
398 are supported by the low correlation found between the pairs of predictors (Fig. S5); only
399 temperatures (minimum and maximum) showed stronger correlation (Pearson's correlation
400 >0.85; Fig. S5), yet the forcing of opposite monotonic trends in the algorithms removed
401 potential confounding effects about their relative contribution (Martins et al., 2021). The
402 models predicted suitable habitats in regions with thermal conditions between 4.45ºC
403 (extreme temperature captured at Tristan da Cunha Island, where the species occurs; Fig.
404 S2) and 21.89ºC, and nutrient conditions of phosphate > 0.13 mmol.m^3 and nitrate > 0.52
405 mmol.m^3. A maximum limit of nutrients was not found along the species distribution.

406 The models revealed that past distributions could have been broader than today (Fig. 2). The
407 equatorial distributional range of *L. pallida* could exceed the current border between Angola
408 and Namibia (LGM ~200km displacement, compared to the present) and the eastward range
409 could have been as far as East London in South Africa (LGM and MH ~750km displacement).
410 The inferred refugial region providing suitable habitats across time included the complete
411 current distributional limits of the species (Fig. 2).

Biophysical modelling

The biophysical model using HYCOM data over the ten-year period released a total of 1,293,162 particles. Particles drifting for the maximum 30-day period connected coastal sites at distances of 82.95±64.53km, on average, with a maximum connectivity distance of 526.50 km (Fig. S6). However, 95% of the connectivity events occurred over distances less than 215 km (Fig. S6).

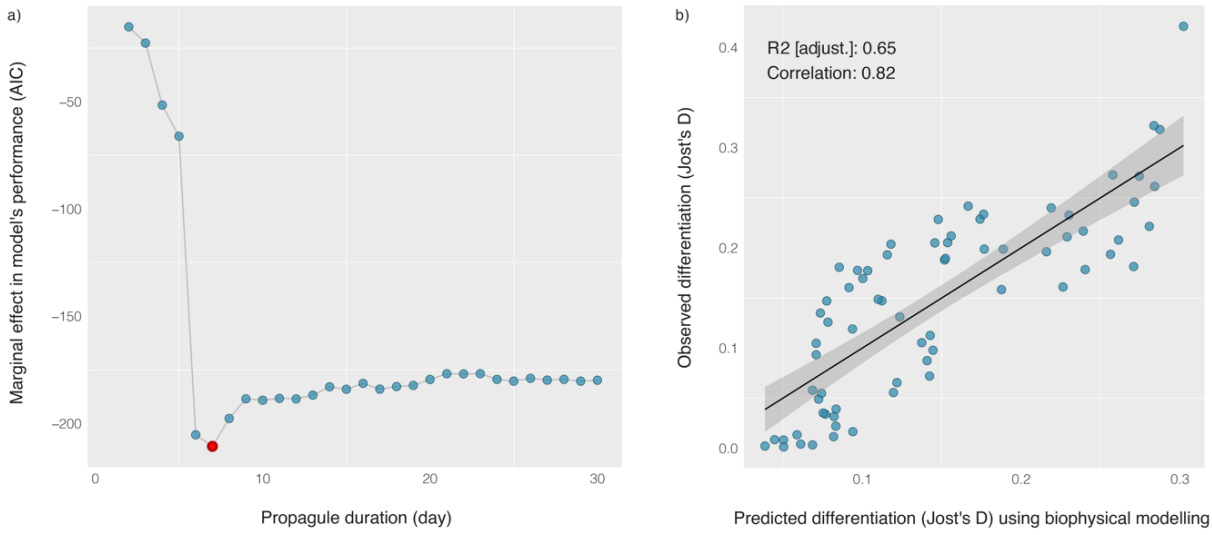


Figure 3. (panel a) Estimation of the potential dispersal period of *Laminaria pallida*. The red dot depicts the most likely dispersal period of the species (minimum AIC at day = 7). (panel b) Linear regression model fitting observed and predicted genetic differentiation (Jost's D) using probability of connectivity constrained to the optimal 7-day propagule duration.

The analysis comparing the marginal effect on AIC between models fitting probability of connectivity and population genetic differentiation identified a 7-day propagule duration for the species (Fig. 3). The connectivity estimates using this period outperformed the null model considering marine distances between paired populations (Fig. 3 vs. Fig. S7), i.e., habitat connectivity driven by ocean transport explained better the variability found in genetic data (adjusted R^2: 0.63; Correlation: 0.81; Fig. 3).

Discussion

By combining empirical genetic data with theoretical modelling, this study demonstrates that along the coastlines of southwestern Africa, intraspecific biodiversity can be highly structured by habitat connectivity driven by oceanographic transport and barriers. In particular, two main genetic clusters were identified, with their break matching a well-known dispersal barrier to marine connectivity (Gunawickrama et al., 2020; Henriques et al., 2012, 2014, 2016; Schulze et al., 2020), i.e., the strong upwelling front centred off Lüderitz. For kelp, an additional constraint to stepping-stone dispersal is the discontinuity of rocky substrate along this coastline. Contrarily to what was hypothesized, the impact of past range shifts might have not been a major driver of the species' genetic structure (Nielsen et al., 2021). The SDM estimated the past distribution of *L. pallida* even broader than today, with none of the present populations potentially affected by extinctions and recolonization processes. No major vicariant events, associated with past sea level changes and coastline displacements, were further predicted. However, genetic diversity patterns are typical of those expected from a lower latitude region that underwent major bottlenecks, as the two well-defined genetic clusters differed strikingly in diversity, with much richer and unique levels in the southern cluster (Namibia South - South Africa), compared to the northern cluster of Namibia North. Limiting habitat conditions along the northern distribution, potentially eroding genetic diversity levels, are hypothesized as the drivers explaining the observed patterns. Although results indicate long-term climate suitability, they are also compatible with the hypothesis of occasional short term heat waves causing local mass mortality events. Other factors, occurring or even intensified in historical times, such as reduced availability of rocky reefs, dust storms decreasing light availability, sand burial and sand scour (Engledow & Bolton, 1994), all likely to impact population sizes, are also compatible with our genetic results. The importance and specific contexts of such events (e.g., in terms of location, timing and intensity) is difficult to hindcast, but genetic diversity asymmetries suggest they have

456 impacted more intensely the northern range. Above all, genetic data reveal two distinct
457 genetic clusters kept genetically isolated by the prevailing oceanographic patterns, giving
458 them high conservation value in the face of future changes.

459

460 **Long-term range stability across past climate changes**

461 The distribution models retrieved good accuracy scores, as expected when fitting machine
462 learning algorithms with compressive occurrence data and biologically meaningful predictors
463 (Assis, Araújo, et al., 2017; M. R. Martins et al., 2021), and the main drivers shaping the
464 distribution of *L. pallida* are corroborated by empirical studies. In particular, the inferred
465 thermal range (between ca. 5 to 22ºC) and nutrient conditions (phosphate > 0.1 and nitrate >
466 1 mmol.m^3) providing suitable habitats match physiological experiments for this species
467 (Martins et al., 2019) and the sister species *L. ochroleuca* (Assis et al., 2018). Transferring the
468 algorithms to past climatologies (MH and LGM) revealed that the distribution of the species
469 might have been broader than today; ~200 km northward during the LGM and ~750 km
470 eastward during both LGM and MH. The northward range shifts likely resulted from the
471 stronger upwelling conditions hypothesized during the LGM for the Benguela region (Romero
472 et al., 2003), while the eastward shifts could have resulted from the weakening of the warmer
473 Agulhas current during both LGM and MH periods (Hutson, 1980; Thackeray, 2016). These
474 historical events might have reduced thermal stress conditions in both warm range edges,
475 allowing range expansions and broadening distribution areas. The recent eastward range
476 expansion of the kelp *Ecklonia maxima* (South Africa), beyond its historical range limit,
477 possibly in response to recent cooling, illustrates well these responses (Bolton et al., 2012).

478 The inferred past range shifts of *L. pallida* contrasts with those reported for numerous kelp
479 species in the North Atlantic, and the Southeast and Northeast Pacific. The current
480 distribution of the species along ca. 2000 km of coastline was predicted to fit entirely within

481 a refugium providing long-term suitability from the LGM to the present. This is a unique case
482 amongst kelps (inc. Laminariales and Tilopteridales; de Bettignies et al., 2021) for which
483 multiple low latitude refugia were identified and corroborated both with SDM and genetic
484 information (Assis et al., 2016, 2018; Fraser et al., 2009; Neiva et al., 2018; Song et al., 2021).
485 Coastline displacements associated with sea level changes could have changed coastal
486 geomorphology and type of substrata, potentially isolating populations of *L. pallida* (Phair et
487 al., 2019; Toms et al., 2014). This was not predicted in our study, but the lack of data
488 describing the past distribution of rocky reefs in the area precludes more accurate estimates.
489 Hence, the models should be interpreted as estimates of fundamental niche conditions, and
490 not fully realized niches. Additional sources of SDM uncertainty that should be acknowledge
491 are related to the algorithms and climatologies used. The ensemble of BRT and AdaBoost,
492 and weighting of different sources of climate data (distinct AOGCMs; Assis, Tyberghein, et
493 al., 2017) allowed the partial assessment of uncertainty (Araújo & New, 2007). Accordingly,
494 the climate data used in SDM mirrored the broadscale patterns of quality-controlled /
495 independent data (Fig. S8). Yet, such independent data is limited to temperature for present-
496 day and LGM conditions. If past conditions in southwestern Africa differed significantly from
497 the patterns described in the data, SDM predictions overestimated actual distributions and
498 therefore potential refugial areas.

499

500 **Ocean currents driving genetic structure of *Laminaria pallida***

501 Our results recovered two well-defined genetic clusters with a region of admixture. These
502 clusters display significant differentiation, suggesting the effect of isolation and drift. Each
503 also contain many private alleles, indicating long-term persistence accumulating mutations
504 that built up endemic diversity. This is in part corroborated by the distribution models
505 predicting stable populations, or at least long-term suitable conditions. But despite such

506 temporal stability, the origin and persistence of the sharp genetic discontinuity must have
507 been shaped by restricted gene flow across both regions, in insufficient levels to counteract
508 genetic differentiation. Our results suggest that long-term oceanographic effects might have
509 played a major role.

510 Biophysical modelling integrating the cartography of rocky substrate largely explained the
511 observed patterns of genetic differentiation, and further suggested the possibility of dispersal
512 by ocean currents up to 7 days. Considering the short spore longevity of kelps (Reed et al.,
513 1992), a lower dispersal period was expected. However, *Laminaria* can be transported as
514 viable floating fragments (Clarkin et al., 2012), which can be even found entangled in rafts of
515 other algae (Susini et al., 2007). This is a well evidenced mechanism of marine dispersal
516 (Clarkin et al., 2012) that might produce rare long-distance connectivity events (Batista et al.,
517 2018), if the rafting fragments contain reproductive structures that release spores after
518 dispersal to suitable areas. The genetic structure of *L. pallida* and other kelp species (Assis
519 et al., 2016, 2018; Neiva et al., 2018) suggest that these events are rare, a premise
520 corroborated by the biophysical modelling (Fig. S6), showing a skewed relationship between
521 probability of connectivity and dispersal distances. The genetic composition of drifting algae,
522 assigned to the adjacent "North Namibia" genetic group, is in line with these predictions.

523 Within the study region, the main mesoscale oceanographic processes revealed in the
524 biophysical modelling to coincide with the species' genetic structure are the strong upwelling
525 conditions centred around the Lüderitz region, which coincides with the main barrier
526 identified in the genetic data, and the prevalent patterns of the Benguela Current, promoting
527 asymmetrical northward flow (Kämpf & Chapman, 2016; Stenevik et al., 2008). While the
528 powerful offshore advection produced along the upwelling cell can generate a barrier to
529 alongshore oceanographic transport, the flow of the Benguela current might homogenize
530 within-cluster genetic structure, a pattern clearly observed in our data, particularly when
531 considering the second level of structure (K=3). Previous studies also suggest that the

Lüderitz upwelling cell constitutes an ancient barrier to gene flow (potentially establishment 2 million years ago; Henriques et al., 2014) that promotes genetic differentiation for numerous species (Gunawickrama et al., 2020; Henriques et al., 2012, 2014, 2016; Reid et al., 2016; Schulze et al., 2020). Indeed, the bioregionalization proposed by (Spalding et al., 2007), separating the Benguela realm into the Namib and Namaqua ecoregions, falls precisely in the region where the main genetic barrier was observed. This strengthens our results, and further supports the role of the Lüderitz upwelling cell in structuring the distribution of biodiversity in southwestern Africa. The discontinuity of rocky shore habitats, also considered in the biophysical modelling, could also play a role in isolation, yet less localized, affecting a broader Namibian coastline. A second level of structure comprising an additional cluster (Southwest Cape) was also identified, but with low statistical support and shallow genetic differentiation. Nonetheless, the genetic barrier identified aligns with a finer scale bioregionalization dividing the Namaqua region from the Southwestern Cape region (Griffiths et al., 2010).

Our results also showed significantly higher and unique genetic diversity along the southern range of *L. pallida*, in Namibia South and South Africa cluster, when compared to the distinct genetic cluster of Namibia North. This is the opposite pattern of that reported for the isopod *Tylos granulatus* along the same stretch of coastline (Mbongwa et al., 2019). As for other *Laminaria* species, long-term persistence of large populations in the southern range might have been crucial to accumulate and preserve genetic diversity (Assis et al., 2018). The lower diversity observed along Namibia North can be explained by three exclusive hypotheses. The first is extinction-recolonization of eroded Namibian habitats post-LGM, that could have produced founder effects and bottlenecks along the colonization front (Assis et al., 2016; Jenkins et al., 2018; Song et al., 2021). However, this finds no support from either distribution modelling, nor the high genetic differentiation found between clusters, with unique alleles also in the northern cluster. The second hypothesis, better supported by genetic evidence,

558 involves demographic effects related to small populations under limiting niche conditions
559 (Nicastro et al., 2013). The centre of the species distribution (circa Lüderitz) experiences
560 maximum monthly temperatures of ca. 15°C, while the northern populations experience
561 temperatures close to the 22°C tolerance limit of the species (as inferred from the models
562 and empirical evidence). Most importantly, heat wave events (Arafeh-Dalmau et al., 2020)
563 and periodic disruptions of the upwelling system (Hutchings et al., 2009) might impact
564 marginal populations due to temporarily reduced availability of cold, nutrient-rich waters.
565 Because no other Laminariales or Fucales (Engledow & Bolton, 1994) exist in northern
566 Namibia region, the potentially lower population sizes are unlikely to result from inter-specific
567 competition. Yet, intensive herbivory may play a role in controlling population sizes at such
568 lower latitudes (Steneck et al., 2017). The third hypothesis has to do with the limitation of
569 rocky shore area through time, along a very sandy coast in Namibia, as well as extinction-
570 recolonization dynamics due to rock burial/exposure. Such effects are likely on the northern
571 Namibian shores and might have taken place at varying degrees, more or less temporary
572 depending on sea-level variation (Peltier, 2004), sand burial of rocky substrate, sand scour
573 by storms, dust storms limiting light and covering rocks, all very limiting factors to persistence
574 of the essential microscopic stages of the kelp life-cycle, the gametophytic generation.

575 Overall, the present study demonstrates how one of the most globally important upwelling
576 systems can favour long-term population persistence, as well as structure oceanographic
577 conditions that create and maintain genetically distinct diversity across distributional ranges.
578 These particular conditions render *Laminaria pallida* a unique case among kelps, for which
579 the entire present distribution range was, according to the models, favourable since the LGM
580 to the present, supporting persisting populations at both range edges, which interestingly are
581 both warmer edges. Additionally, the oceanographic barrier posed by the upwelling might
582 have shaped the main genetic discontinuities of the species, which further coincided with
583 well-known biogeographic subdivisions. Considering the recent and projected intensification

584 of these conditions (Sydeman et al., 2014), it is likely that the observed genetic traits of
585 *Laminaria pallida*, as well as those of species with similar niche requirements and
586 distributions, will persist for the years to come (Lourenço et al., 2016), again contrasting with
587 what has been observed and anticipated for numerous kelp forest species elsewhere (Arafeh-
588 Dalmau et al., 2020; Assis, Araújo, et al., 2017). Despite the general stability trend, the
589 northernmost populations, with already reduced diversity levels, are prone to climate change
590 impacts (Potts et al., 2014) and associated biodiversity losses, from the genetic to the
591 ecosystem level. The distinct genetic diversity inferred between regions, coupled with the
592 sharp isolation of phylogroups highlight their high conservation value in the face of future
593 changes, particularly given the multiple ecological, social, and economic services provided
594 by kelp forests (Blamey & Bolton, 2018) (Blamey & Bolton, 2018). As recently proposed for
595 the region and elsewhere (Mertens et al., 2018; Nepper-davidsen et al., 2021), specific
596 management and conservation actions might be required for divergent genetic lineages, as
597 distinct drivers influence their levels of genetic diversity. The insights provided here are a
598 significant step forward in the understanding of patterns and processes influencing marine
599 biodiversity in southwestern Africa, and we hypothesize that they might be generalizable for
600 other species with limited dispersal potential, which have been particularly overlooked in the
601 region.
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Data availability statement

All data described in the Material and Methods section are openly available in Figshare at: https://doi.org/10.6084/m9.figshare.17075177

Biosketch

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