

Antarctica's ecological isolation will be broken by storm-driven dispersal and warming

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Antarctica has long been considered biologically isolated¹. Global warming will make parts of Antarctica more habitable for invasive taxa, yet presumed barriers to dispersal—especially the Southern Ocean's strong, circumpolar winds, ocean currents and fronts—have been thought to protect the region from non-anthropogenic colonizations from the north^{1,2}. We combine molecular and oceanographic tools to directly test for biological dispersal across the Southern Ocean. Genomic analyses reveal that rafting keystone kelps recently travelled >20,000 km and crossed several ocean-front 'barriers' to reach Antarctica from mid-latitude source populations. High-resolution ocean circulation models, incorporating both mesoscale eddies and wave-driven Stokes drift, indicate that such Antarctic incursions are remarkably frequent and rapid. Our results demonstrate that storm-forced surface waves and ocean eddies can dramatically enhance oceanographic connectivity for drift particles in surface layers, and show that Antarctica is not biologically isolated. We infer that Antarctica's long-standing ecological differences have been the result of environmental extremes that have precluded the establishment of temperate-adapted taxa, but that such taxa nonetheless frequently disperse to the region. Global warming thus has the potential to allow the establishment of diverse new species—including keystone kelps that would drastically alter ecosystem dynamics—even without anthropogenic introductions.

Antarctica broke from its last Gondwanan connection (South America) over 40 million years ago³, and has long been considered biologically isolated from the rest of the world¹. Antarctica's terrestrial and marine ecosystems have high levels of endemism⁴, and the Southern Ocean's strong, circumpolar winds and ocean currents have been inferred to preclude passive southward dispersal of organisms into the Antarctic^{1,2}. The onset of deep-reaching flow of the Antarctic Circumpolar Current (ACC) created a barrier to poleward heat transport across the Southern Ocean⁵, and the strong, circumpolar thermal fronts have also been inferred to represent an impenetrable physical barrier for most organisms. Indeed, there has been almost no evidence of biological movement into the Antarctic from lower latitudes since the Last Glacial Maximum

(LGM)⁶, except via anthropogenic dispersal⁷. Phylogenetic analyses indicate that the Southern Ocean has, in the millions of years since the breakup of Gondwana, occasionally been traversed by marine (for example, refs ^{8–10}) and terrestrial taxa (for example, refs ^{11,12}), but no natural colonizations are known to have occurred since the LGM, except by elephant seals¹³. Benthic crabs reported to have invaded the Antarctic slope in recent decades are now thought to have been in Antarctic waters for millions of years¹⁴. However, recent observations of rafting sub-Antarctic biota south of the Antarctic Polar Front (APF)¹⁵ provide tantalizing indications that these ocean fronts might indeed be permeable. The APF is nonetheless only one of several presumed frontal barriers to southward movement in the Southern Ocean (Fig. 1), and whether biological material can disperse from northern (sub-Antarctic and temperate) landmasses to Antarctica, against the prevailing eastward currents and winds, remains unclear. With parts of Antarctica among the most rapidly warming regions on Earth¹⁶, and increasing evidence that the Antarctic is fast becoming hospitable to diverse taxa from lower latitudes^{17,18}, there is a pressing need to reassess the extent of Antarctica's biological isolation.

Here, we report direct evidence that passively dispersing surface-drift biological material can reach Antarctica from lower latitudes. We used population genomic analyses to pinpoint the origins of non-Antarctic kelp rafts recently collected from Antarctic beaches. Such rafts represent buoyant substrata for diverse invertebrate and algal communities¹⁹, and thus are potential vectors for biological colonization of Antarctica. In early 2017, thalli of the keystone southern bull kelp *Durvillaea antarctica*—a buoyant species with a cold-temperate and sub-Antarctic distribution that is absent from Antarctica and all islands south of the Southern ACC Front—were collected from beaches on King George Island, Antarctica (62°S) (Fig. 1c). One thallus had large goose barnacles (*Lepas australis*) attached to it (maximum 10.5 mm capitulum)—a biological signature of lengthy time adrift at sea¹⁹. Genomic analyses (15,994 single nucleotide polymorphisms (SNPs)) of these beach-cast specimens, together with samples from established populations throughout the species' range (Supplementary Table 1), show that they rafted to Antarctica from two different mid-latitude source populations (Kerguelen (49°S) and South Georgia (54°S)) (Fig. 1a,b and

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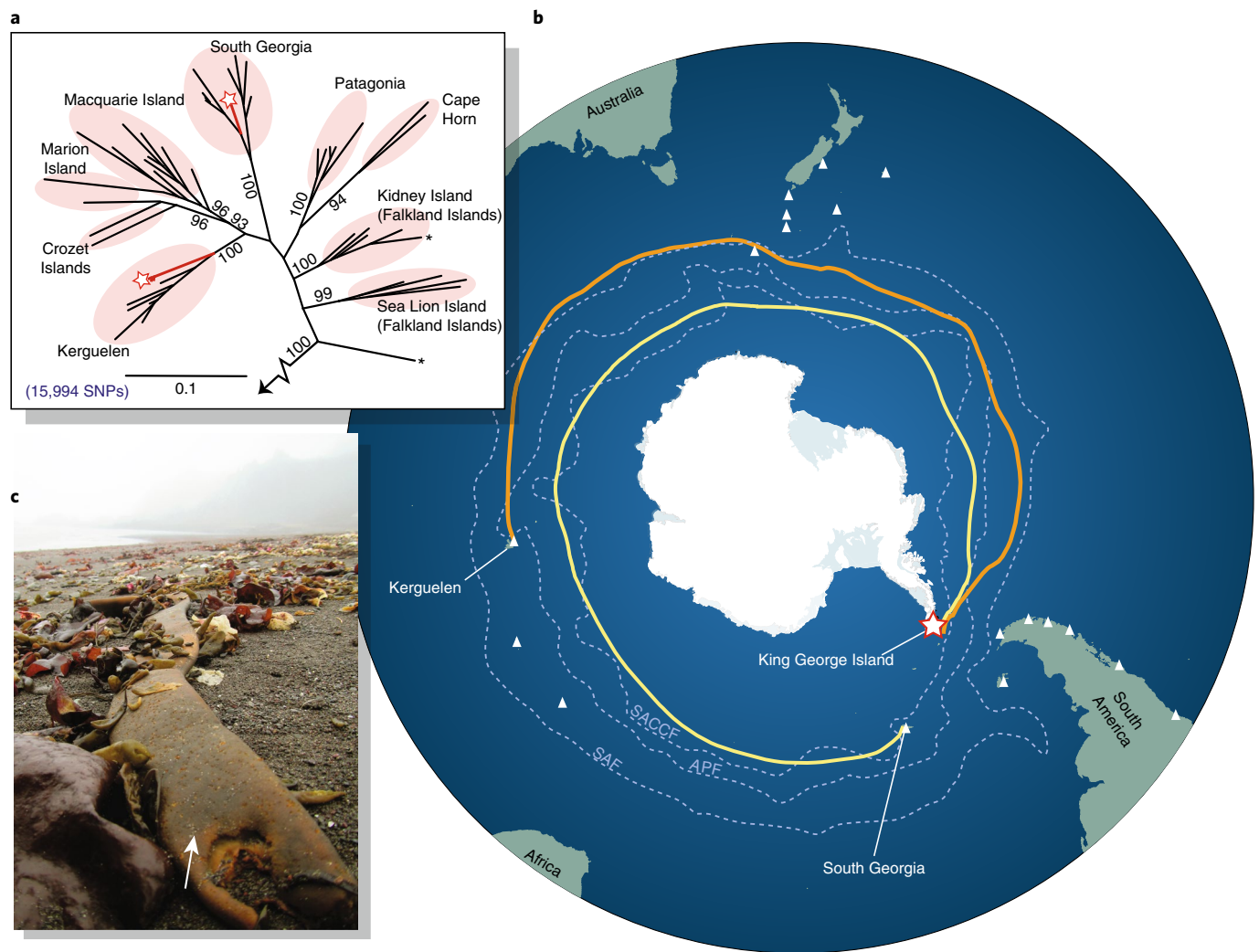


Fig. 1 | Genomic analyses reveal that mid-latitude (Kerguelen, South Georgia) kelp dispersed thousands of kilometres to reach the Antarctic coast.

a, Unrooted phylogeny (SNP data) for the 'greater sub-Antarctic' clade. Red branches and stars represent drift material from King George Island, Antarctica. The asterisks represent Kerguelen samples that grouped with other regions. For the complete phylogeny, including temperate locations, see Supplementary Fig. 1. **b**, Locations of samples included in genomic analyses (white triangles), representing the entire range of the species. The orange and yellow lines show the average simulated dispersal routes for kelp released from Kerguelen and South Georgia, respectively, that reached Antarctica near King George Island. The mean positions of major fronts (the APF, Southern ACC Front (SACCF) and sub-Antarctic Front (SAF); calculated from HYCOM data (see Methods)) are shown. **c**, Beach-cast *D. antarctica* specimen at King George Island (indicated by an arrow).

Supplementary Fig. 1). Importantly, both specimens were reproductively viable, with male conceptacles containing mature antheridia.

Rafting *D. antarctica* is known for its capacity to transport diverse holdfast biotas (including molluscs, arthropods and echinoderms) across oceans¹⁹, and is frequently observed drifting in the Southern Ocean; indeed, there are an estimated 70 million specimens of this buoyant kelp species drifting north of the Polar Front at any time, 20 million of which have holdfasts still attached²⁰. Frequent dispersal of this species to Antarctica could thus facilitate incursions of entire coastal benthic communities, mirroring the post-LGM assembly of sub-Antarctic island marine ecosystems^{6,21}. Establishment of large, keystone kelp species in Antarctica would have major ecological flow-on effects, just as past climate-driven shifts in kelp-associated communities dramatically altered coastal productivity in temperate regions²². The discovery of *D. antarctica* specimens arriving at King George Island raises the question: are such rafting events anomalous, or is dispersal of drift material to Antarctica frequent?

We tested the dispersal of surface-bound material using a Lagrangian analysis of eddy-resolving ocean circulation model

simulations (see Methods). The model output includes a fully developed mesoscale eddy field, recently inferred to play a key role in shallow-water marine organisms crossing the APF^{15,23}. The model velocities are combined with the nonlinear wave-driven advection of Stokes drift, which arises from the action of wind on the ocean and transports material at the surface in the direction of wave propagation. In regions with large wave climates, such as the Southern Ocean, Stokes drift could have a strong influence on surface particle movement. Indeed, the significance of Stokes drift at the surface in the Southern Ocean can be seen from a comparison of satellite-tracked drifting buoys with drogues attached (15 m depth) and without drogues attached (closer to the surface) (Supplementary Fig. 2; see also Methods). The Lagrangian analysis shows that substantial numbers of particles released from South Georgia (Fig. 2 and Supplementary Video 1) and Kerguelen (Supplementary Fig. 3) were able to cross the Southern Ocean fronts. For example, from South Georgia, 0.19% of all released particles ultimately reached the Antarctic shelf (Fig. 2c). When either Stokes drift (Fig. 2a) or eddies (Fig. 2b) were eliminated from the simulation, no

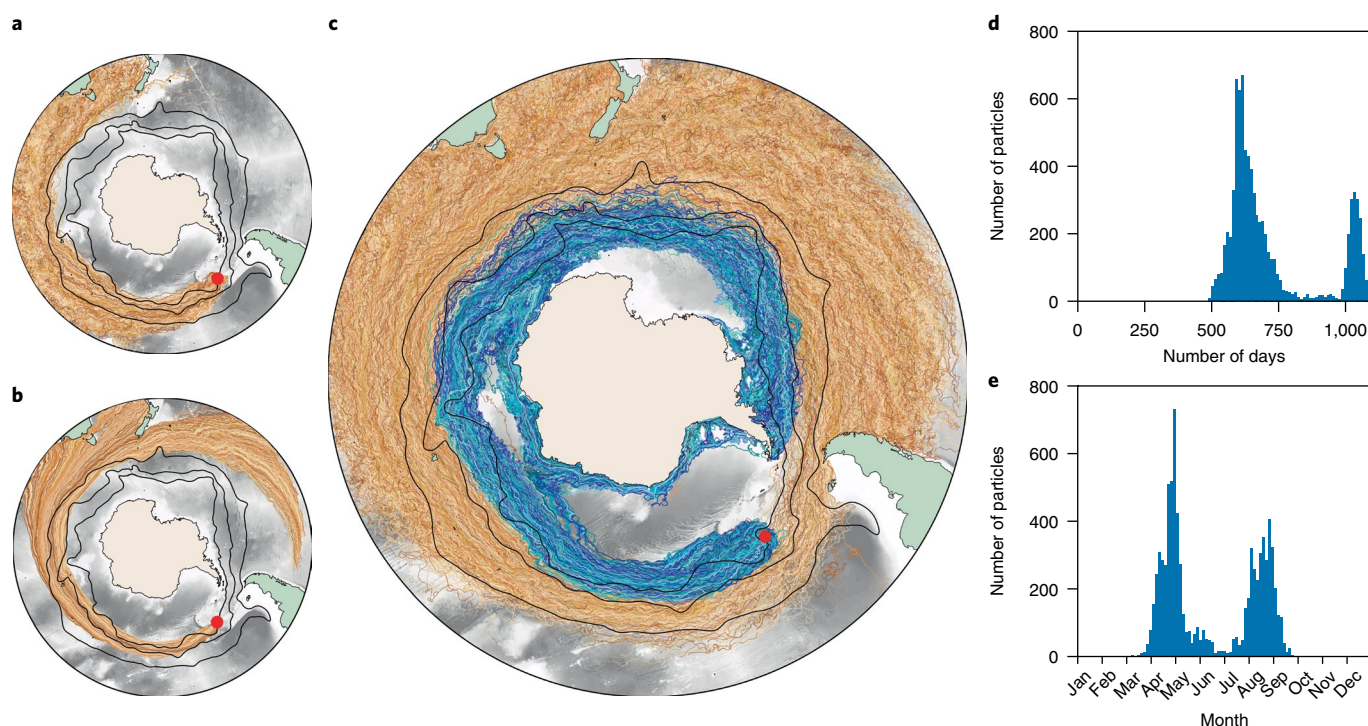


Fig. 2 | Simulated drift particle trajectories from South Georgia. **a–c**, More than 4.2 million particles were released from South Georgia (red dot) and advected for 3 years with simulated surface ocean velocities where: **(a)** eddies, but not Stokes drift, were incorporated; **(b)** Stokes drift, but not eddies, was incorporated; and **(c)** both Stokes drift and eddies were incorporated. Blue lines show trajectories for all particles located on the Antarctic continental shelf after three years. Brown lines show trajectories for a random sample (0.1%) of particles not satisfying this condition. Black lines indicate the mean positions of major fronts (see Fig. 1) based on HYCOM data from 2013–2016 (see Methods). **d,e**, Histograms show the number of days for the particles shown by the blue trajectories in **a–c** to reach Antarctica (**d**) and the time of year that the particles that did reach Antarctica were released from South Georgia (**e**).

particles reached the Antarctic coastline. Many particles that reached Antarctica had common release dates (Fig. 2e), implying that many particles crossed en masse, perhaps during major storms (by ‘storms’, we mean atmospheric variability—both cyclones and anticyclones). Further assessment showed that, indeed, particles that reached Antarctica experienced large southward Stokes velocities, consistent with strong storm conditions (Supplementary Fig. 4). We tested connectivity with Antarctica for two other release locations (Macquarie Island (Supplementary Fig. 5) and southern South America (Supplementary Fig. 6)) and found that in all cases, some particles (0.0001–0.1915%) were able to reach the Antarctic coast within the three-year period (Table 1). Our circumpolar at-sea surveys, comprising data from more than 15,000 km of observational transects in the 2016/2017 Austral summer, also revealed large numbers of this kelp species in cold, ‘Antarctic’ waters $<4^{\circ}\text{C}$ (Supplementary Fig. 7), further indicating that Antarctic incursions can readily occur.

The estimated dispersal timeframe from sub-Antarctic to Antarctic shores was often brief enough to be biologically plausible (Fig. 2d). Specifically, 72% of the drift particles from South Georgia that reached Antarctica did so within 2 years, and some in as few as 489 days (travelling at mean speeds of up to 0.43 m s^{-1} , which are comparable with ACC jet surface speeds of $0.1\text{--}0.6\text{ m s}^{-1}$; ref. ²⁴). *D. antarctica* lives for several years, and many of its invertebrate passengers are brooding taxa whose offspring could remain on a drifting raft for multiple generations¹⁹. Detached macroalgal rafts survive well in cold waters, maintaining reproductive capacity and tissue growth²⁵. Our results therefore indicate that reproductively viable shallow-water marine communities could rapidly establish in Antarctica with ameliorating climatic conditions. Furthermore, these analyses highlight the potential for a wide variety of floating material (from seeds and driftwood to plastics) to traverse the Southern Ocean.

Table 1 | Summary data for all particle releases used in the ocean drift simulations

Release location	Total number of particles released	Number of particles reaching Antarctica within 3 years	Percentage of particles reaching Antarctica within 3 years	Minimum days to reach Antarctica	Minimum km to reach Antarctica
Kerguelen	3,906,194	5	0.0001	546	20,445
South Georgia	4,286,085	8,206	0.1915	489	10,472
Macquarie Island	4,729,019	30	0.0006	319	10,824
Chile	3,882,775	510	0.0131	573	13,771

There is increasing recognition that transoceanic rafting events can play (and have played) an important role in global biogeography^{26,27}. The dispersal distances documented here represent the longest biological rafting events ever recorded, at more than 20,000 km from Kerguelen to the maritime Antarctic Peninsula region via the shortest simulated route, and mean trajectory distances of more than 25,000 km for specimens originating in South Georgia (Fig. 1b). The only comparable recorded drift distances are of *Nothofagus* driftwood suspected to be from South America reaching Tasmania (approximately 15,000 km to the east) in 1955²⁸, and pumice believed to be from a volcano in the South Sandwich Islands reaching New Zealand (~13,000 km to the east) a little over 2 years after a 1962 eruption²⁹. Our capacity to confidently pinpoint the sources of such long-distance dispersal events has now improved dramatically with the advent of genomic technologies that can resolve fine-scale structure within species.

Our results indicate that non-anthropogenic biological dispersal to Antarctica via rafting is frequent, and that the establishment of non-native species is thus presumably prevented by the environment rather than transport. Indeed, the extreme conditions that currently prevail in much of coastal Antarctica, with cold temperatures, little available ice-free terrain, and scouring by sea ice and icebergs, presently preclude the establishment of numerous 'temperate' taxa. In particular, large kelp species such as *D. antarctica* and *Macrocystis pyrifera*, and the diverse epibiotic communities that associate with these taxa, are absent from regions affected by extensive ice scour, although they can survive in partially glaciated regions and near-freezing water temperatures²¹. Antarctic intertidal ecosystems are starkly different from those of the sub-Antarctic. Those in the Antarctic are inhabited by small, short-lived macroalgae and motile invertebrates that can shelter from ice scour in rock crevices, while those in the sub-Antarctic are dominated by large brown algae that provide habitat for a wide range of invertebrates³⁰. However, modelling has indicated that some parts of the marine shelf in Antarctica—especially along the West Antarctic Peninsula—could, by the end of this century, experience warming that would greatly reduce the survival of many Antarctic marine species and facilitate survival of sub-Antarctic taxa¹⁸. Species such as *D. antarctica* and *M. pyrifera* might then be able to survive along Antarctic coasts in bays and other areas protected from extensive ice scour. With our models indicating that the coasts of the continent are frequently reached by floating biological material pushed across the Southern Ocean by strong winds and storms, we predict that there will, in the coming decades, be establishment of diverse non-native taxa in Antarctica.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available at <https://doi.org/10.1038/s41558-018-0209-7>.

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Author contributions

C.I.F. and J.M.W. conceived the research. A.K.M., E.v.S. and A.M.H. conducted all oceanographic modelling. P.G.R. conducted the at-sea kelp surveys. E.C.M. and N.V. discovered and identified the drift samples from beaches in Antarctica. C.I.F. sourced (and in most cases, collected) the kelp samples used in the genomic analyses, and directed the genomic laboratory work carried out by A.P. C.J. contributed bioinformatics expertise and ran the genomic analyses. C.I.F. wrote the first draft of the paper. All authors contributed to editing the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Methods

Genomic analyses. Tissue samples of southern bull kelp (*D. antarctica*) were collected between 2006 and 2010 from established populations in 18 regions throughout the entire species' range. We here analysed samples from all genetic lineages resolved in earlier analyses of mitochondrial, nuclear and chloroplast markers³¹, including the New Zealand clade (South Island, North Island, Chatham Islands and Bounty Islands), central Chilean clade (southern-central Chile) and sub-Antarctic clade (Chilean Patagonian fjords, Antipodes Islands, Campbell Island, Crozet Islands, Falkland Islands, Gough Island, Kerguelen Marion Island, Macquarie Island, Snares Islands and South Georgia). Wherever possible, samples were included from more than one locality in each region. Tissue was stored at room temperature, desiccated over silica gel beads. DNA was extracted from 167 samples from the established populations. A full list of locations and numbers of samples from which DNA was extracted is provided in Supplementary Table 1. DNA was also extracted in triplicate from dried samples of each of two beach-cast specimens of *D. antarctica* that were collected on King George Island, Antarctica, in early 2017 (specimen 1 was collected on 21 January from 62° 12' 43.66" S, 58° 57' 37.48" W; specimen 2 was collected on 12 February from 62° 10' 27.70" S, 58° 58' 13.04" W; for both specimens, pieces ~3 cm × 3 cm had been preserved by desiccation over silica gel beads). Microscopic observations of reproductive structures in the samples found at King George Island were made using fresh or rehydrated pieces of tissue: sections were hand-cut using a razor blade, and observed with an Olympus CX31 microscope.

Genomic DNA was extracted from desiccated kelp tissue using the PowerPlant Pro Kit with subsequent purification using the PowerClean Pro Kit (Qiagen) (following ref. ³²), but using ~1 mm² of dried tissue from each sample, incubated for 2 h at 65 °C in deionized water before DNA extraction.

SNP data were obtained via genotyping-by-sequencing³³. Genotyping-by-sequencing library preparation followed standard protocols³³ with modifications. To each DNA sample, a uniquely barcoded PstI adapter was added (2.25 ng per sample)³⁴. Digestion was performed with 4 U PstI-HF (New England Biolabs) in 1× CutSmart Buffer, and incubated at 37 °C for 2 h. Adapters were ligated with T4 DNA ligase in 1× ligation buffer (New England Biolabs) and incubated at 16 °C for 90 min (with 2 min at 37 °C every 30 min) and 80 °C for 30 min. Purification was carried out using a Qiagen MinElute 96 UF PCR Purification Kit (Qiagen), with elution in 25 µl 1× TE. PCRs were run on 50 µl volumes containing 10 µl purified DNA, 1× MyTaq™ HS Master Mix (Bioline) and 1 µM each of PCR primers 5' AATGATACGGCGACCACCGAGATCTACACTCTTCCCTACACGACGCTCTTCCGATC*T and 5' CAAGCAGAAGACGGCATACGAGATCGGTCTCGGCATTCCTGCTGAACCGCTCTCCGATC*T (where * indicates phosphorothioation) at 72 °C for 5 min, 95 °C for 60 s, and 24 cycles of 95 °C for 30 s, 65 °C for 30 s and 72 °C for 30 s, with a final extension step at 72 °C for 5 min. Concentrations for each sample were assessed using a LabChip GXII (Caliper Life Sciences) and pooled equimolarly. A 200-base pair (bp) fraction (from 250–450 bp) of the pooled library was separated via electrophoresis on a 1.5% agarose gel. Sequencing of DNA from this size range was carried out on one lane of a high-output flowcell in an Illumina NextSeq 500 system (75 bp paired-end).

Combinatorial barcoded read pairs were demultiplexed with AXE³⁵. Illumina TruSeq3 adapters were clipped, and reads were merged and truncated (based on quality scores) to 64 bases using Trimit, producing 575,969,634 reads. Reads were assembled into clusters and SNP loci were detected de novo using Stacks³⁶. We retained reads that: (1) were present in at least 20% of samples within each regional group; (2) were detected in at least 2 regional groups; (3) had a rare allele frequency of at least 20%; (4) had a minimum coverage of 10 reads; and (5) had no more than 2 alleles detected. Samples that contained fewer than 5% meaningful loci were removed, leaving 101 samples (including 3 replicates of 1 raft sample, and 1 replicate of the other, from King George Island) and 15,994 SNP loci. Phylogenetic reconstruction was performed using IQ-Tree³⁷ with free-rate model testing using ModelFinder³⁸ and 1,000 bootstraps³⁹. Scripts are provided in a public repository (see Data availability).

At-sea surveys of drift kelp. Drifting kelp individuals were counted during daylight steaming throughout the Antarctic Circumnavigation Expedition from 21 December 2016 to 19 March 2017. The *Akademik Tryoshnikov* travelled from Cape Town to Hobart via Marion Island, Iles Crozet, Iles Kerguelen and Heard Island, then from Hobart to Punta Arenas via the Mertz Glacier, Balleny Islands, Scott Island, Mount Siple, Peter I Øy and Diego Ramirez, and then from Punta Arenas to Cape Town via South Georgia, the South Sandwich Islands and Bouvetoya (route shown in Supplementary Fig. 7). All kelp rafts were recorded on continuous transects during daylight (up to 16 h per day, depending on latitude and season) while the ship moved at 11–15 knots (20–28 km h⁻¹). Observations were made from the ship's bridge (14 m above sea level) or bow (7 m above sea level) on the side of the ship that offered the best visibility. Distant individuals were counted by scanning with binoculars, but 96% of *D. antarctica* plants were within 100 m of the ship's track (and 84% were within 50 m). A simple index of the relative abundance of *D. antarctica* was derived as the number of plants per 100 km of transect per day. Days with less than 50 km of transect were discarded.

The observation days were assigned a representative location by averaging the longitudes and latitudes at the start and end of the observation time. These

locations were then used to estimate local sea surface temperature, by linear interpolation of the sea surface temperature field of the Hybrid Coordinate Ocean Model (HYCOM) + Navy Coupled Ocean Data Assimilation Global 1/12° Analysis⁴⁰ onto the dates and locations of the observations. This HYCOM dataset assimilates observational data from satellites, Argo floats and other instruments, and is designed to be as similar to real ocean flow as possible.

Lagrangian oceanographic modelling. Lagrangian analysis was used to assess the capacity of drift biological material sourced from non-Antarctic waters to reach the Antarctic coast. More than 3.8 million virtual particles were released from a 2° latitude by 4° longitude box surrounding each of four sub-Antarctic source locations. The four release locations included the two source regions (South Georgia and Kerguelen) of the kelp specimens found on King George Island (determined via genomic analyses), as well as the two most southerly sites within the normal distributional range of *D. antarctica*: Macquarie Island and Cape Horn. The number of particles released from each location differs (see Table 1) because, for some locations, significant land area covers the 2° by 4° box. However, for all release locations, at least 3.8 million particles were released. Particles were released daily throughout 2013 to sample seasonality and storm variability. Virtual particles were advected offline for three years from the time of release using the connectivity modelling system (CMS⁴¹). The time step for particle advection in CMS was two hours. Particles were advected with the sum of daily snapshots of two-dimensional surface (1 m depth) velocity data from an eddy ocean model (HYCOM) and wave-driven Stokes drift velocities from WAVEWATCH III. HYCOM is a publicly available 1/12° global ocean model analysis⁴⁰ that incorporates the combined effect of wind stress and large-scale ocean currents, constrained by data assimilation techniques. However, the modelled velocity field does not resolve surface waves, which generate nonlinear Stokes drift in a thin surface layer. Stokes drift velocities from the same period (2013–2016) of a global hindcast⁴² of WAVEWATCH III forced with Climate Forecast System Reanalysis were used. The three-hourly Stokes drift velocities were combined into daily averages and interpolated onto the HYCOM grid.

Particles were considered to reach Antarctica if they remained on the Antarctic continental shelf (defined using the 1,000 m isobath) at the end of the 3 years of advection. Many more particles, compared with the numbers listed in Table 1, crossed the edge of the continental shelf, particularly near the tip of the Antarctic Peninsula, but were swept away again rapidly by the ACC. For the modelling to be relevant for potential colonization by kelp, we chose only to consider the smaller subset of particles that remained on the continental shelf three years after release. To analyse the impact of surface waves on the particle connectivity, we repeated the particle release experiments using only the surface velocities from HYCOM (Fig. 2a). The effect of eddy variability was assessed by advecting particles using four-year mean velocities from HYCOM, combined with the time-varying Stokes drift velocities (Fig. 2b).

The Southern Ocean fronts shown in the figures were calculated from HYCOM sea surface height (SSH), averaged over the period 2013–2016. At a particular longitude, the largest meridional gradients in SSH were identified. This procedure was repeated at a number of meridional transects, and the individual transect values were averaged to find circumpolar values of SSH for each front.

Drifter analysis. Satellite-tracked drifting buoys (drifters) were compared with simulated particles to test the importance of including Stokes drift in our calculated trajectories. Data from the Global Drifter Program were analysed for 2 sets of drifter trajectories—those with drogues attached (centred at 15 m depth; 'drogued') and those without drogues ('undrogued'). Stokes drift decays rapidly with depth; for example, for waves with 10 m wavelength, the Stokes drift is reduced to less than 10% of its surface value at 2 m depth. Undrogued drifters can therefore be expected to experience strong effects of Stokes drift, but drogued drifters will be much less affected by Stokes drift. We selected all daily segments of trajectories starting within a given 3° latitude band, and analysed the resulting latitudinal distribution of these trajectories 1 year later (Supplementary Fig. 2). The initial latitude bands were selected to cover the range of kelp release locations (49–56° S). We repeated the same analysis for simulated particles (trajectories were included from all four release locations) advected with and without Stokes drift.

The distributions of drogueless drifters shifted notably southward after one year of travel, compared with drifters with drogues attached. Thus, particles close to the surface behaved differently compared with those at 15 m depth. These results are consistent with our modelling results, which show that adding Stokes drift shifts the particle distributions southward, mimicking the effect of drifters losing their drogues. The distributions of drogued drifters were shifted slightly further southward compared with the modelled particles without Stokes drift, but this is not unexpected because there is still an influence of Stokes drift at 15 m depth (particularly for waves with long wavelengths; for example, for a wavelength of 100 m, the Stokes drift is 15% of its surface maximum at 15 m depth). Furthermore, the determination of whether or not (and when) a drifter has lost its drogue is imperfect, and some of the drifters listed as drogued might have lost their drogues⁴³ and thus experienced a greater influence of Stokes drift.

Data availability. Genomic data (raw reads) have been deposited in the NCBI Sequence Read Archive (accessions SRS2559675–SRS2559863,

SRR6123253–SRR6123419 and SRX3235906–SRX3236072; see Supplementary Table 1). At-sea survey data are provided in Supplementary Table 2. HYCOM velocity data are available from <https://hycom.org/dataserver/gofs-3pt0/analysis/>. Stokes drift velocities estimated by WAVEWATCH III are available from <ftp.ifremer.fr/ifremer/ww3/HINDCAST/GLOBAL/>. Drifter trajectory data are available from the Global Drifter Program at <http://www.aoml.noaa.gov/phod/dac/index.php>. Genomic analysis scripts are provided in the public repository at https://bitbucket.org/cameronjack/gbs_fraser_kelp. The CMS particle advection code is available from <https://github.com/beatrixparis/connectivity-modeling-system>.

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