



RESEARCH ARTICLE

An integrated ecological, genetic and geological assessment of long-distance dispersal by invertebrates on kelp rafts

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Abstract. Long-distance dispersal (LDD) is thought to be a key driver of biogeographic processes, yet few direct natural observations have been made of this process. Several studies have characterised diverse benthic epibiotic communities associated with buoyant macroalgae and have proposed that kelp rafting may be an important LDD mechanism for such coastal species. We test for LDD by combining biological, genetic, and geological data from rafted bull-kelp (*Durvillaea antarctica*) specimens collected in southern New Zealand following a March 2018 storm. Genetic and ecological data strongly indicate that three of 29 detached kelp specimens sequenced (and their associated live epifaunal taxa) had rafted from the sub-Antarctic to mainland New Zealand, traversing both oceanographic and phylogeographic barriers, over the course of an approximately 4-week journey. Numerous additional epifaunal taxa were detected from rafts that had geologically-distant mainland origins. The successful trans-oceanic rafting documented for sub-Antarctic brooding sea-star, chiton and sea-slug taxa presents a mechanism for their broad but phylogeographically disjunct Southern Hemisphere distributions. Moreover, the detection of several such LDD events over the last decade suggests that such journeys are very common over evolutionary timeframes. Although geological and genetic data were informative over different scales, we detected no conflict between the inferences from these distinct data sets, a finding that reinforces the value of integrative approaches to marine biogeography.

Keywords: Long distance dispersal, biogeography, connectivity, genetics, marine, phylogeography, rafting, storms.

Introduction

Long-distance dispersal (LDD) has long been considered an important but rare biogeographic process (Darwin 1859, Nathan 2006, Jordano 2017) that may influence both ecological and evolutionary phenomena (Kinlan et al. 2005, Gillespie et al. 2012, Shaw and Gillespie 2016). Direct evidence for natural LDD, however, has often proven elusive, with observations sometimes perceived as anecdotal (e.g., Helmuth et al. 1994, Censky et al. 1998). LDD can be defined as the process whereby individuals of a species move beyond their 'genetic neighbourhood' (e.g., haplogroup boundaries) and cross substantial geographic boundaries to reach new, distant terrain (see Jordano 2017). Although a few biogeographers have discounted the importance of LDD (e.g., Heads 2005), many researchers remain intrigued by processes whereby non-dispersive taxa can achieve vast and dynamically shifting geographic distributions (De Queiroz 2005, Yoder and Nowak 2006, Gillespie et al. 2012).

In recent decades, several researchers have suggested that rafting on natural, buoyant substrata appears

to have been a key LDD mechanism for numerous widespread but coastally restricted lineages ('Paradox of Rockall': Johannesson 1988, Ó Foighil et al. 1999, Ali and Huber 2010). Several recent studies have placed particular emphasis on the potential role of floating macroalgae (Highsmith 1985, Ingólfsson 1995, Fraser et al. 2011) as vectors for trans-oceanic LDD. While recently documented cases of anthropogenic rafting of pelagically-developing taxa on artificial substrata provide evidence for increasing human impacts on marine ecosystems (e.g., Thiel and Gutow 2005, Carlton et al. 2017), the potential ongoing role of natural substrata as facilitators of LDD of strictly coastal species that lack intrinsic LDD capacities remains unclear, with few compelling direct observations of such processes (e.g., where raft origins are known; but see Fraser et al. 2011).

The Southern Ocean encircles Antarctica and comprises tens of thousands of kilometres of open ocean punctuated only by a series of tiny, isolated oceanic and continental islands (Fig. 1a). Despite their geographic isolation, Southern Ocean coasts

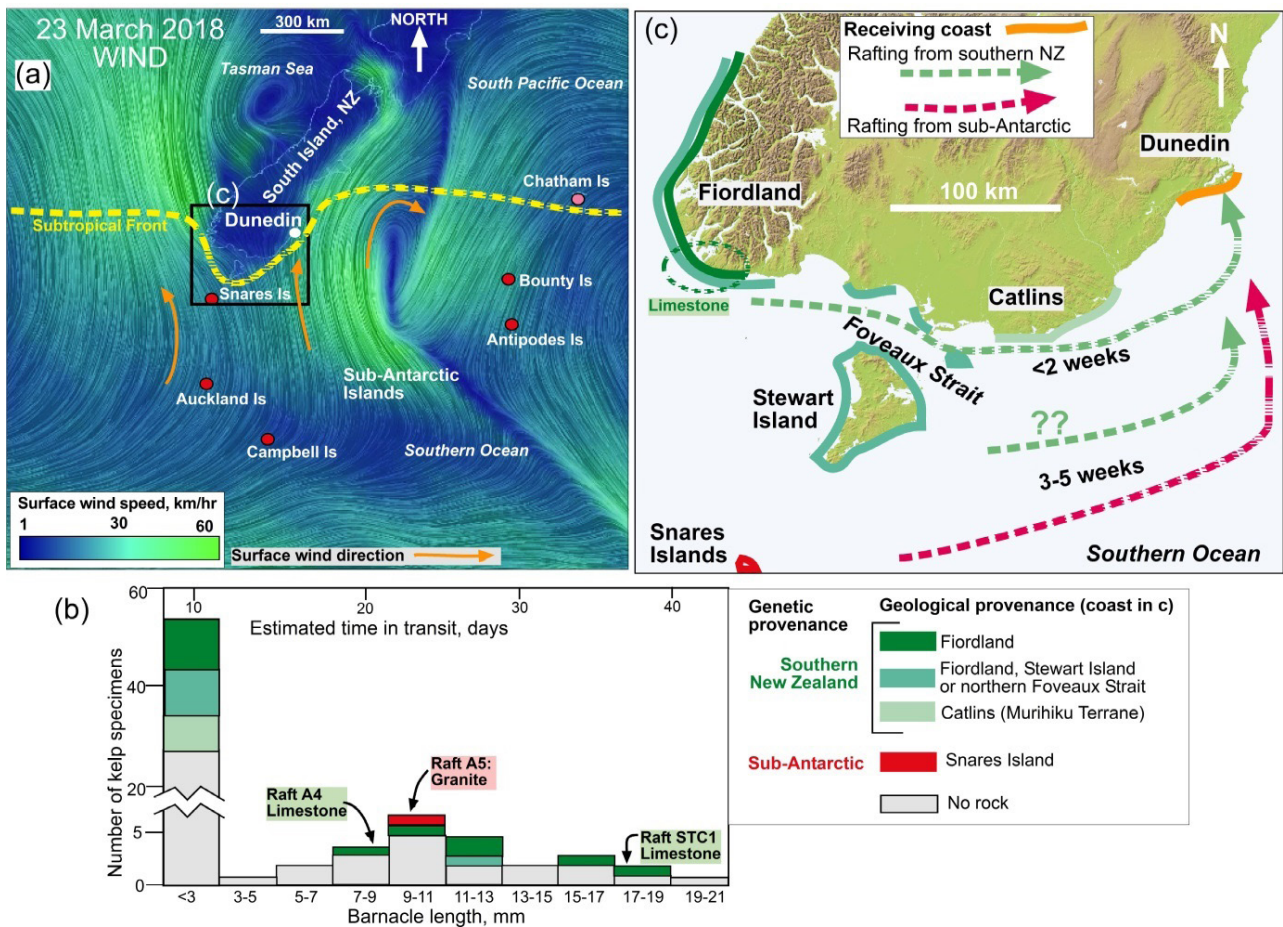


Figure 1. Geological and biological evidence for long-distance dispersal of Southern Ocean kelp rafts. (a) Geographical setting in southern New Zealand and the Southern Ocean, with wind speeds and directions (from <https://earth.nullschool.net>) for the late March 2018 storm that caused abundant far-travelled kelp rafts to beach near Dunedin city. (b) Histogram of maximum *Lepas australis* barnacle lengths on kelp rafts (and inferred travel time), with inferred sources based on rocks on holdfasts. (c) Inferred travelling trajectories of kelp rafts based on geological sources and barnacle lengths.

share numerous intertidal and shallow subtidal species (Fraser et al. 2009a, 2013, Macaya and Zuccarello 2010, Nikula et al. 2010, Cumming et al. 2014, González-Wevar et al. 2018). Some of the islands are geologically young – several are only a few hundreds of thousands of years old (see Chown et al. 2008) – and could therefore only have been colonised via transoceanic dispersal. A number of recent studies have sought to understand the processes that might facilitate LDD among such disjunct sub-Antarctic coastal regions (Chiswell 2009, Reisser et al. 2011, Cumming et al. 2014, González-Wevar et al. 2018 – and reviewed by Moon et al. 2017). Large, detached specimens of buoyant kelp (*Durvillaea* and *Macrocystis*) are abundant in the Southern Ocean (Smith 2002, Fraser et al. 2017), and these macroalgae have been suggested to be important vectors for passive LDD of coastal species (e.g., Edgar 1987, Highsmith 1985, Donald et al. 2005). In particular, *Durvillaea antarctica* is a buoyant, habitat-forming, benthic kelp species that dominates mid- to high-latitude coasts of the Southern Hemisphere (Fraser et al. 2009a), and many millions of rafts of this species are adrift in

the Southern Ocean at any time (Smith 2002). While the trajectories of such rafting events are typically constrained by oceanographic features such as the Subtropical Front (Fig. 1a; Garden et al. 2014), major storms can overcome the influence of such barriers for surface-drift material (Waters et al. 2018a, Fraser et al. 2018a). Additionally, while individual studies provide anecdotal support for rafting of kelp (Fraser et al. 2018a, Waters et al. 2018a) and associated invertebrate taxa (Fraser et al. 2011, Waters et al. 2018b), and oceanographic simulations suggest that LDD rafting events could occur frequently (Fraser et al. 2018a), an assessment of the frequency and number of taxa involved in such rafting has been lacking.

Here we combine biological, genetic, and geological data to test the geographic origins and dispersal distances of kelp-rafts driven ashore in southern New Zealand by a major storm in March 2018 and provide a brief assessment of the numbers of diverse, large epifaunal invertebrate specimens transported by long-distance rafting.

Methods

Raft sampling

The current study was facilitated by the arrival of anomalously abundant rafted kelp (*D. antarctica*) specimens on beaches near Dunedin city in southeastern New Zealand, after a major storm event in late March 2018 (Fig. 1a). The tail end of the March storm involved a prolonged period (>24 hours) of strong southeasterly winds (Fig. 1a) that facilitated the beaching of the kelp assessed in this study, as has occurred for several recently-documented storms (Waters et al. 2011, 2018a). Although we inspected approximately 250 beach-cast *Durvillaea* specimens (Table S1), our study focusses primarily on detecting long-distance epifaunal rafting, and thus we used the following sampling criteria. First, we closely inspected only the kelp specimens ($n = 155$; Table S1) that had been colonised by *Lepas australis* barnacles - a signature of substantial time adrift at sea (Skerman 1958; Fig. 1b; see below). Of these 155 *Lepas*-covered specimens, we subsequently focussed on only those carrying live benthic epifauna ($n = 40$) and/or exhibiting holdfast rocks of non-local origin ($n = 37$) (Table S1). In the field, large epifaunal invertebrates (primarily Mollusca) were removed from the external surfaces of *Lepas*-covered *Durvillaea* holdfasts using forceps, and placed in labelled plastic bags, together with reference *Durvillaea* tissue samples, the five largest *Lepas* individuals present, and rock samples (if present) for each raft. All samples were stored frozen prior to laboratory analysis. While every effort was made to collect any large, externally visible holdfast molluscan and echinoderm taxa, holdfasts were not dissected in the field, and thus small boring epifaunal arthropod taxa such as *Limnoria* and *Parawaldeckia* (Nikula et al. 2010, Fraser et al. 2011) were not sampled. Our sampling also ignored benthic barnacles, epibiotic macroalgae, bryozoans, and cnidarians for which regional phylogeographic data are lacking and for which we would therefore not be able to determine origins.

Geological origins of rafts

Kelp holdfasts of *D. antarctica* commonly retain rock fragments from the site of their original attachment, and these can provide a physical basis for assigning rafted kelp to distinctive geological source regions (Garden et al. 2011). As this study aimed to identify cases of LDD, we did not sample 'local' kelp specimens (lacking *Lepas* barnacles) and we similarly ignored specimens bearing rocks from the immediate vicinity of the receiving coastline around Dunedin (Fig. 1a, c), which include distinctive schist and basalt fragments. By contrast, kelp specimens bearing distinctive rocks from more remote geographic sources were sampled and assigned to their source regions (see Fig. 1b, c; Table S3). We used mineral composition of holdfast clasts (see Table 2 of Waters and Craw 2018) to assess the geographic origins of non-local kelp specimens based on distinctive regional geological features that have been compiled by Turnbull and Allibone (2003) and Turnbull et al. (2010).

The nearest set of rocks that are readily distinguished from locally-derived Dunedin rocks are in the Catlins area (Fig. 1c, pale green coast). These include lithified greywackes, argillites, vitric tuffs, and conglomerates (Turnbull and Allibone 2003; Waters and Craw 2017). South and west of the Catlins area, the Foveaux Strait, Fiordland, and Stewart Island coastlines consist of a range of granitoid and related igneous rocks (Fig. 1c, mid-green coasts; Turnbull and Allibone 2003; Turnbull et al. 2010), and more specific localization of rock sources is generally not possible. Coarse-grained high-grade metamorphic rocks, including gneisses and garnet-bearing amphibolites, occur only along the southwestern coast of Fiordland (Fig. 1c; dark green coast). Similarly, distinctive limestones and related sedimentary rocks occur on the coastline in a limited area of southwestern Fiordland (Fig. 1c, green dashed ellipse; Carter and Lindqvist 1975, Waters and Craw 2018). However, these rocks also occur on Campbell Island in the Southern Ocean (Fig. 1a; Beggs 1978).

Barnacle colonisation and rafting duration estimates

Objects drifting at the sea surface are rapidly colonised by obligate epifaunal *Lepas* barnacles, and the capitulum length of attached *Lepas* can represent a proxy for an object's time at sea (Skerman 1958, see equation in Fraser et al. 2011). Indeed, previous studies from southern New Zealand have shown strong associations between genetically-determined raft origins and the size of attached *L. australis* (Waters et al. 2018a). We used *L. australis* growth data from southern New Zealand (Skerman 1958) to estimate the age of the largest *L. australis* specimen on each kelp raft and thereby estimate minimum rafting duration (see equation in Fraser et al. 2011, Waters and Craw 2017, 2018).

Genetic origins of kelp rafts and epifauna

A well-constrained phylogeographic distinction has been defined for *D. antarctica* between southern New Zealand (including Stewart Island) and the outlying sub-Antarctic islands of the Southern Ocean (Fraser et al. 2009, 2011, Bussolini and Waters 2015, Waters et al. 2018b), and this disjunction was used as a primary criterion for distinguishing mainland-origin versus sub-Antarctic-origin kelp specimens. Protocols for *Durvillaea* DNA extraction, PCR and sequencing of mitochondrial COI primers followed Fraser et al. (2009b). Protocols for DNA extraction DNA and mtDNA COI sequencing of epifaunal molluscan taxa followed Nikula et al. (2014) and Cumming et al. (2014). Sequence data were edited and aligned in Geneious R11 (<https://www.geneious.com>), and BLAST searches were used to compare sequences against previously published data. Haplotype networks (Fig. 2) were constructed with PopArt 1.7 (Leigh and Bryant 2015; <http://popart.otago.ac.nz>) incorporating new sequence data alongside previously-detected COI haplotypes for kelp *D. antarctica* (GenBank details from Bussolini and Waters (2015) and Waters et al. (2018b)), the sea-slug *Onchidella marginata* (GenBank details from Cumming et al. 2014), and the chiton *Onithochiton neglectus* (GenBank details from Nikula et al. 2013).

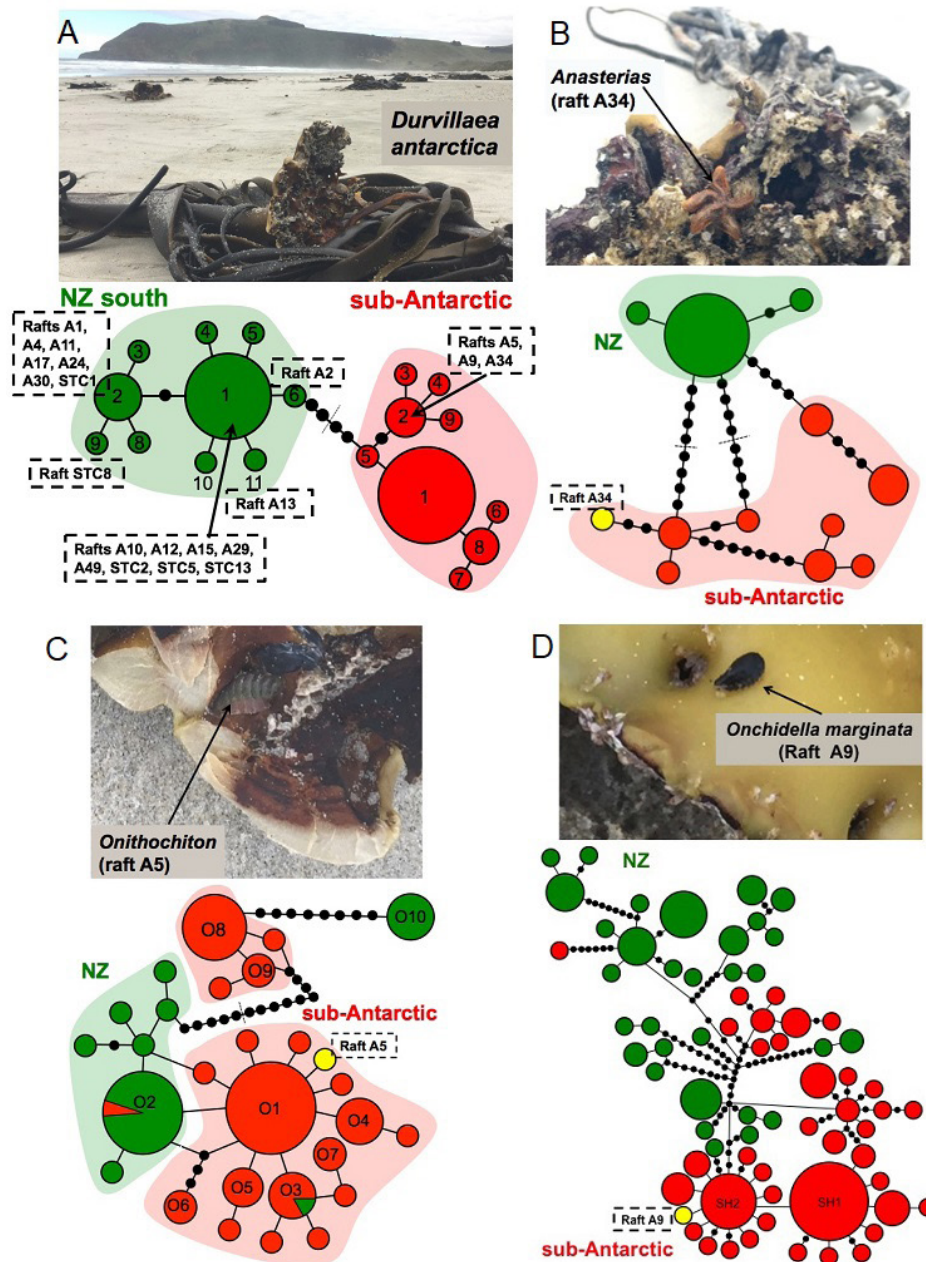


Figure 2. Genetic evidence for trans-oceanic dispersal of sub-Antarctic kelp and epifauna. Phylogenetic networks of mtDNA COI haplotypes showing differentiation between mainland New Zealand (NZ; green) versus sub-Antarctic and Chatham Island (red) populations of (a) bull-kelp *Durvillaea antarctica*; (b) the Southern Ocean sea-star *Anasterias*; (c) the widespread chiton *Onithochiton neglectus*; and (d) the Southern Ocean gastropod *Onchidella marginata*. Epifaunal specimens inferred to have been transported from the sub-Antarctic to mainland New Zealand by kelp rafts A5, A9 and A34 are indicated in yellow.

Origins of the rafted sea-star *Anasterias* were similarly inferred by phylogenetic analyses of mtDNA. This brooding sea-star genus has a circumpolar distribution in the Southern Hemisphere, encompassing numerous sub-Antarctic islands in addition to the southern New Zealand mainland (Waters et al. 2018b). Total DNA was extracted from tube feet of the beach-cast *Anasterias* specimen from kelp raft A34 using Chelex (Walsh et al. 1991). DNA was extracted from tube feet of benthic *Anasterias* specimens previously collected from

Durvillaea antarctica holdfasts across the Southern Ocean, including the Chatham Islands, Auckland Islands, Campbell, Bounty, Crozet and Kerguelen islands (details in Fig. S1). PCR amplification and sequencing of mtDNA COI was performed using primers F210 and COIA (primer sequences and thermal cycling conditions following Waters and Roy (2004)). Minimum spanning networks were constructed from COI sequences using PopArt 1.7. Phylogenetic analyses of *Anasterias* were conducted with the inclusion of previously published

COI sequences from New Zealand *Anasterias* and other Southern Ocean Asteroiidae taxa (Mah and Foltz 2011, Waters et al. 2018b). We used the automated model selection option of PAUP* (Swofford 2016) to choose a model of sequence evolution for maximum likelihood (ML) analysis using the Akaike information criterion (nst=2; unequal basefreq). The ML tree was reconstructed using PAUP* with the full heuristic search option and 20 replicates of random sequence addition. Phylogenetic support for each node was assessed using 500 bootstrap replicates (Felsenstein 1985). *Anasterias*, *Onchidella* and *Onithochiton* DNA sequences new to this study are available on GenBank (accessions MK160621-MK160632).

Results

Geological origins and rafting durations of beach-cast kelp specimens

In March 2018, thirty-seven of the 155 *Lepas*-covered (reflecting substantial time adrift at sea) kelp rafts inspected retained distinctive holdfast rock fragments indicating remote geological origins (Fig. 1b, c). Of the exotic rafted rock specimens, six were derived from the geologically distinctive Catlins region, 100 km to the southwest of the Dunedin beaches where they were blown ashore (Fig. 1b-c). By contrast, 31 beach-cast specimens were derived from more distant sources, some of which were >400 km away (Fig. 1b-c). While 23 of these rafted specimens from the Fiordland and Foveaux regions exhibited small *Lepas* barnacles (<3 mm; estimated rafting journeys <12 days; Fig. 1b), eight yielded substantially larger *Lepas* (7-19 mm) (Fig. 1b).

Of the rocks indicating the most distant mainland (Fiordland) origins for sampled kelp rafts, the most distinctive clasts are fine-grained (micritic) limestones with abundant microfossils and fine detrital carbonaceous matter. Genetic sequencing of kelp rafts bearing these limestones yielded mainland haplotypes; Fig. 1a-c; Table S3). Additionally, coarse-grained garnet-bearing gneiss fragments on kelp holdfasts are distinctive high-grade metamorphic rocks from the Fiordland basement. These gneissic fragments match source rocks from the same general area as the limestones in southwestern Fiordland and/or from the Fiordland coast further to the northwest (Fig. 1c). One distinctive granite clast (raft A5) contained both muscovite and biotite, a relatively rare occurrence in the region (Table S3, Fig. S2). Genetic data from the hosting kelp support derivation of this granite from Snares Islands (Table S3) rather than Fiordland or Stewart Island. Apart from this latter specimen, most of the granitoid rock fragments sampled from beach-cast kelp specimens were not distinctive apart from indicating a general distant (>200 km) southwestern provenance (Fig. 1b-c).

Diverse rafting epifauna

In total, we retrieved 66 invertebrate specimens from the holdfasts of 40 *Lepas*-covered beach-cast *Durvillaea* specimens sampled in March 2018 (variously estimated to have been at sea between 10 days and

6 weeks; Fig. 1b). The rafted invertebrate assemblage comprised 13 benthic epifaunal species (12 molluscan species and 1 echinoderm; Table S2). The most frequently-detected species were the widespread sub-Antarctic New Zealand chiton *Onithochiton neglectus* (21 individuals, 13 separate rafts) and the New Zealand limpet *Siphonaria australis* (20 individuals across 10 rafts). An additional four molluscan taxa were found on multiple rafts: the circumpolar brooding sea-slug *Onchidella marginata* (Cumming et al. 2014), two New Zealand chiton species of the genus *Plaxiphora*, and the widespread blue mussel *Mytilus galloprovincialis*.

Trans-oceanic dispersal of sub-Antarctic rafts and epifauna

Sub-Antarctic kelp *Durvillaea* (rafts A5, A9, A34): Of the 29 *Lepas*-covered *Durvillaea* specimens from which high-quality DNA sequences were obtained (details summarised in Table S3), 18 yielded haplotypes characteristic of the 'NZ South' (mainland) *D. antarctica* clade (Fig. 2a) and a further eight yielded sequences of *D. poha* (for which species genetic analyses are not currently able to distinguish among geographic regions). By contrast, three rafts (A5, A9 and A34) yielded the distinctive sub-Antarctic *D. antarctica* kelp haplotype Subant-2, characteristic of the Snares and Auckland Islands.

Sub-Antarctic sea-star *Anasterias* (raft A34): Phylogenetic analysis based on novel mtDNA COI data from across the range of *Anasterias* (including Kerguelen and Crozet islands; Fig. S1) supported a consistent genetic distinction between sub-Antarctic versus mainland New Zealand benthic specimens (*A. suteri*). The beach-cast *Anasterias* COI haplotype clustered within the widespread 'sub-Antarctic' COI haplogroup, phylogenetically distinct from mainland New Zealand *A. suteri* (Fig. 2b, Fig. S1). The hosting kelp raft A34 yielded the sub-Antarctic kelp haplotype Subant-2; (Auckland and Snares islands; Bussolini and Waters 2015), and an estimated rafting duration of 26 days (Table S3).

Sub-Antarctic chiton *Onithochiton* (raft A5): The single *O. neglectus* specimen found on sub-Antarctic-origin kelp raft A5 (kelp haplotype Subant-2; estimated rafting duration 25 days) yielded a novel haplotype closely related to widespread but sub-Antarctic-limited haplotype O1 (Fig. 2c; Table S3).

Sub-Antarctic sea-slug *Onchidella* (raft A9): The single *O. marginata* specimen found on sub-Antarctic-origin kelp raft A9 (kelp haplotype Subant-2; estimated rafting duration 29 days) yielded a novel haplotype that clustered with the sub-Antarctic haplogroup of this species (Fig. 2d; Table S3).

Genetic origins and rafting duration of mainland-origin epifauna

Cantharidus roseus

The single specimen of trochid gastropod *Cantharidus roseus* (retrieved from kelp raft A15, maximum *Lepas australis* 2.4 mm; estimated rafting duration 11 days) yielded the common haplotype C7, previously detected

only on the New Zealand mainland (Nikula et al. 2013). The hosting kelp raft yielded a mainland haplotype (haplotype NZ South 1) and mainland geological clasts (Fiordland/Southland) (Table S3).

Onithochiton neglectus

This chiton species is a common component of the benthic *Durvillaea* holdfast community (Morton and Miller 1973; Fig. 4). Of the 20 *O. neglectus* specimens collected from mainland-origin kelp rafts (STC6, STC8(6), STC16, A10, A13, A27(3), A29, A33, A38, A43, A44, A45, A47), 8 were sequenced. The six individuals retrieved from kelp raft STC8 (kelp haplotype NZ-South 9; *Lepas australis* 19.7 mm, estimated rafting duration 42 days; Table S3) shared a previously undetected haplotype.

Onchidella marginata

Two mainland-origin rafts (STC13: *Lepas* 2.4 mm; A48: *Lepas* 2.0 mm; Table S3) yielded specimens of *O. marginata*, the latter raft yielding three specimens of this gastropod. Specimens from both rafts yielded haplotypes that were similar or identical to common mainland haplotypes of this species (Cumming et al. 2014).

Sypharochiton sinclairi

This holdfast-dwelling chiton (Nikula et al. 2011; Fig. 4) was detected on a single raft (STC7) estimated to have been at sea for approximately 10 days (*Lepas* size 1.9 mm).

Discussion

Our study reveals passive rafting of several kelp-associated benthic invertebrate species from the sub-Antarctic to the mainland coast of New Zealand. This direct documentation of oceanic rafting (Fig. 3) – whereby non-dispersive, brooding coastal invertebrate species raft on natural substrata, traversing a major oceanographic barrier (the Subtropical Front; Fig. 1a; Garden et al. 2014), to reach shores beyond their phylogeographic range – clearly satisfies recent ecological definitions of long-distance dispersal (Jordano 2017). These findings further highlight the apparent role of storm events in facilitating LDD across prevailing oceanographic barriers (Monzón-Argüello et al. 2012, Waters et al. 2018a, Fraser et al. 2018a). Additionally, these new data complement the findings of several previous studies showing the arrival of sub-Antarctic *D. antarctica* to mainland New Zealand (Collins et al. 2010, Fraser et al. 2011, Bussolini and Waters 2015, Waters et al. 2018, Fig. 3) and also provide new examples of epifaunal taxa that had not previously been detected traversing major oceanographic barriers.

A combination of genetic, biological and geological evidence (Fig. 2, Table S3) suggests that three sub-Antarctic kelp rafts (A5, A9, and A34) and their epifauna likely had similar geographic origins. First, all three kelp specimens share the phylogeographically distinctive sub-Antarctic *D. antarctica* haplotype (Subant-2; Fig. 1a), known only from kelp populations in the Auckland and Snares Islands (Bussolini and Waters, 2015). These three

rafts also have very similar rafting duration estimates (25–29 days) based on the size of attached *Lepas*. Given these similar timeframes, the distinctive geology of rocks attached to raft A5 (Snares granite rather than Auckland Islands granite), and congruent sub-Antarctic genetic origins for rafted epifauna *Onithochiton* (A5), *Anasterias* (A34) and *Onchidella* (A9), we conclude that all three specimens are most likely to have originated from the Snares Islands and completed the >400 km journey essentially simultaneously. These parallel dispersal events are thus estimated to have covered approximately 14–16 km day⁻¹, comparable with the findings of Fraser et al. (2011) who suggested that drifting sub-Antarctic specimens had rafted to Dunedin from at least as far away as the Snares (~400 km) at speeds averaging approximately 0.2 m s⁻¹ (17 km day⁻¹).

While not all of the 13 benthic rafting taxa detected in March 2018 (Table S2) have well-characterised life histories, several are definitively brooders, including two taxa with circumpolar distributions for which kelp rafting has previously been suggested as a key biogeographic explanation: *Anasterias* (O'Hara 1998, Waters et al. 2018b) and *Onchidella marginata* (Cumming et al. 2014). Additionally, a further two taxa are strictly non-pelagic yet widespread across southern New Zealand and its isolated sub-Antarctic islands (the gastropod *Cantharidus roseus* and the brooding chiton *Onithochiton neglectus*; Nikula et al. 2013) (Figs. 2, 3, 4). These four epifaunal species all commonly occur in the benthic *Durvillaea* holdfast community (Morton and Miller 1973; Fig. 4), and all four have previously been detected in *Durvillaea antarctica* rafts (Fraser et al. 2011; Waters et al. 2018a, b). Additionally, each of the aforementioned molluscan taxa exhibits only minimal nuclear genetic differentiation among disjunct sub-Antarctic and mainland localities (Nikula et al. 2013; Cumming et al. 2014).

The finding that all three sub-Antarctic benthic invertebrate lineages that successfully dispersed across the Subtropical Front to mainland New Zealand in early 2018 (*Anasterias*, *Onchidella*, *Onithochiton*) are brooding taxa, builds on the inferences of Fraser et al. (2011) and Nikula et al. (2013) regarding LDD of similarly non-pelagic taxa (e.g., *Limnoria*, *Parawaldeckia*, *Cantharidus*) in 2009–2010 (Fig. 3). Such successful rafting of otherwise non-dispersive taxa may help explain the 'Paradox of Rockall' (Johannesson 1988), whereby 'low-dispersal' marine taxa can have anomalously broad geographic distributions. In some cases, LDD of such taxa may be aided by the possibility of multiple generations occurring over the course of a single rafting journey (Nikula et al. 2013, Cumming et al. 2014). Notably, it has been suggested that oceanic rafting may facilitate dispersal over vast spatial scales (e.g., >1000 km: Thiel and Haye 2006; and even tens of thousands of kms: Fraser et al. 2018a), distances that are broadly unattainable via conventional pelagic larval dispersal (e.g., Nickols et al. 2015).

By assessing both the point-of-origin and age of rafting events, we are able to demonstrate their biological plausibility (i.e., with rafted kelp and passengers having survived the journey). We also suggest that this rafting

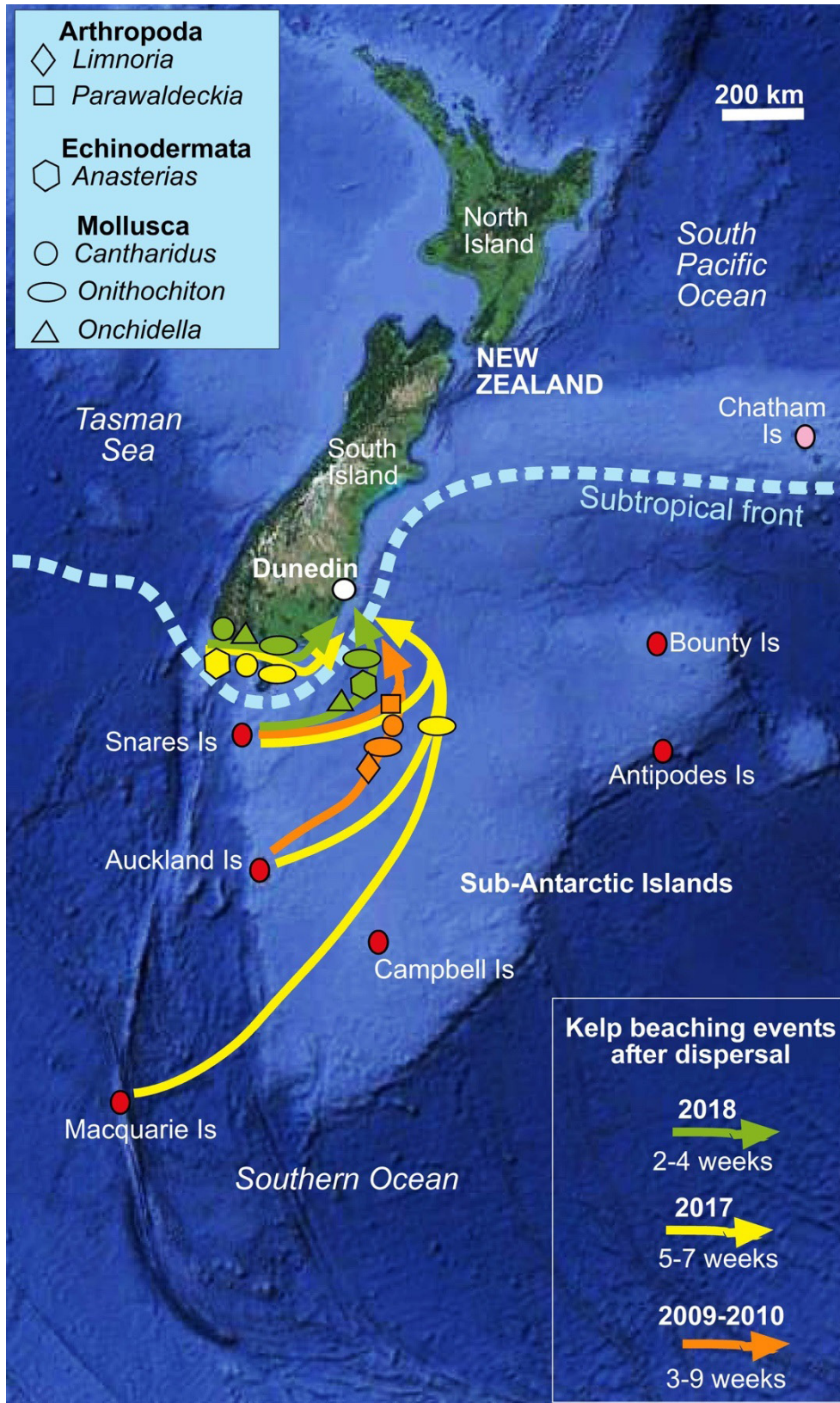


Figure 3. Summary of coastal and trans-oceanic LDD of detached kelp (*Durvillaea antarctica*; coloured arrows) and associated brooding benthic epifauna (coloured symbols) detected by Fraser et al. 2011, Waters et al. 2018a, b, and the current study. Estimated rafting durations (in weeks) based on the size of attached *Lepas australis* barnacles are indicated inset. All of the non-dispersive littoral taxa illustrated here are distributed widely across the Southern Ocean’s isolated sub-Antarctic islands, although most have mtDNA phylogeographic breaks (Fig. 2) delineated by the Subtropical Front oceanographic barrier (dashed line).



Figure 4. Southern New Zealand's distinctive *Durvillaea antarctica* holdfast invertebrate assemblage (see also Morton and Miller 1973). All seven of these epifaunal taxa were detected in the holdfasts of beach-cast *Durvillaea* in the current study (Table S2), having completed extended rafting journeys at sea (as evidenced by distinctive genetic and geological origins as well as *Lepas australis* colonisation of their rafts). Photos modified from personal or creative commons sources: *Sypharochiton sinclairi*: Jon Sullivan; *Plaxiphora boydeni*: Peter Poortman, www.nzshells.net.nz; *Onithochiton neglectus*: Priscilla Salloum; *Anasterias*: Jonathan Waters; *Siphonaria*: Naturalis Biodiversity Center/Wikimedia Commons; *Onchidella*: Peter Harrison/Wikimedia Common; *Cantharidus*: Jan Delsen/Wikimedia Commons; *Durvillaea antarctica* wrack: Ceridwen Fraser.

mechanism can explain both the wide distributions of many brooding benthic taxa and the postglacial colonisation of Southern Ocean coastal ecosystems (Fraser et al. 2009, 2018a). For instance, the rafting of a sub-Antarctic lineage of the southern brooding sea-star *Anasterias* to mainland New Zealand may represent an analogue for the original expansion of this genus into the northernmost part of its range (Fig. S1). In such cases, the presence of already-established, ecologically similar congeneric/conspecific lineages likely reduces the opportunities for successful establishment of such secondary dispersers (i.e., 'founder takes all'; Waters et al. 2013, Fraser et al. 2018b).

By combining ecological, geological and genetic data, we show the potential of these diverse data types to together provide an integrated assessment

of rafting journeys. The different data types carry their own strengths and limitations. While the mtDNA genetic data, for instance, are particularly useful for discriminating broad regional sources of kelp rafts and their epifauna (e.g., sub-Antarctic versus mainland; Fig. 2), geological data are often more informative for discriminating among relatively fine-scale geographic source regions (e.g., different terranes within mainland New Zealand; Fig. 1b; Table S3; Waters et al. 2018a). Importantly, our study detected no cases of substantial or unresolvable conflict between geologically- versus genetically-inferred raft sources, a finding that supports the reliability of both approaches. However, the future application of more powerful, genome-wide approaches will enhance the potential for genetically assigning rafts to more precise source localities (e.g., specific

islands and/or more localised coastal source regions; Fraser et al. 2018a), potentially even exceeding the high geographic precision sometimes achievable from distinctive local rock units.

The observed bimodal *Lepas* size-frequency distribution on beach-cast rafts (Fig. 1b; Table S1) suggests either that there were two distinct geographic source regions for southern mainland kelp rafts, or that rafting journeys can be complex given temporal variation in meteorological and oceanographic conditions (e.g., Fig. S3). As suggested by Fraser et al. 2011, different macroalgal rafts might become detached from the coast at different places and times yet arrive at a destination simultaneously.

Our study reveals a species-rich rafting assemblage comprising coastal taxa that are primarily limited to intertidal and/or shallow subtidal benthic substrata. Microhabitat preferences have been suggested to be a useful predictor of a species' rafting potential (Donald et al. 2005, Nikula et al. 2011), and the current study may add some weight to this suggestion. Specifically, a sizeable proportion of the rafted invertebrate taxa detected in March 2018 (Fig. 4) are also common components of New Zealand's benthic *Durvillaea* holdfast community (see Morton and Miller 1973). We suggest that macroalgal holdfast-dwelling taxa are particularly likely to be dispersed by kelp rafting. Additionally, while LDD is often characterised as a stochastic process, the trajectories and distances involved can be predictable to some extent based on abiotic features (e.g., meteorological and oceanographic data; Fig. 1a; Collins et al. 2010, Garden et al. 2014, Waters et al. 2018a), and the species involved are somewhat predictable on the basis of ecological (Fig. 4) and life history traits (Gillespie et al. 2012, Shaw and Gillespie 2016).

While scientists have long debated the plausibility of long-distance rafting playing a major role in shaping species distributions (de Queiroz 2005), direct evidence for this process is increasing. In particular, direct documentation of numerous natural long-distance kelp rafting events over the last decade (e.g., Fraser et al. 2011, López et al. 2018, Fraser et al. 2018a, current study), together with recent population-genetic inferences of this process (e.g., Ó Foighil et al. 1999, Haye et al. 2012, Nikula et al. 2013, Smith et al. 2018), are shedding new light on the potential frequency (e.g., ecological timescales) and broad scale (e.g., trans-oceanic) of natural LDD events affecting Southern Hemisphere coastal biogeography.

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Supplementary Material

Supplementary material accompanies this paper.

Table S1. Summary of beach-cast *Durvillaea* sampling at three Dunedin beaches following the March 2018 storm event. To avoid beach-cast material of local origin, sampling was restricted to specimens covered in *Lepas australis* barnacles, and with a primary focus on specimens bearing exotic holdfast rocks and/or visible benthic epifauna.

Table S2. Details of 13 live benthic invertebrate taxa retrieved from 40 beach-cast bull-kelp (*Durvillaea*) rafts on Dunedin beaches following the storm of March 23, 2018. All sampled rafts were covered in *Lepas australis* barnacles, indicating substantial periods adrift at sea.

Table S3. Summary of 29 beach-cast kelp rafts for which genetic data were obtained (*Durvillaea* haplotype names and GenBank accession codes indicated). The three rafts inferred to have sub-Antarctic origins (kelp haplotype SA2) are highlighted with grey shading. Rafting durations (days) were estimated from the maximum capitulum length (mm) of attached *Lepas australis* barnacles. Geological origins of rafts were further inferred from rock clasts attached to kelp holdfasts. Raft codes indicate collection locality (Allans Beach (A); St Clair (STC)).

Figure S1: Maximum likelihood phylogeny of *Anasterias* COI sequences, showing a phylogenetic distinction between sub-Antarctic versus mainland New Zealand (NZ) samples. Southern Ocean asteriid outgroup taxa (*Notasterias*, *Diplasterias*, *Psilidaster*; Mah and Foltz 2011, Waters et al. 2018b) are removed for diagrammatic purposes. Numbers at nodes represent bootstrap support values over 75%. The analysis supports the non-mainland origins of *Anasterias* from kelp raft A34 (pictured), which washed ashore in southern New Zealand in March 2018. In addition to reference mainland NZ (TA, AB, VB, PR, FS) and Auckland Islands (CH) samples previously sequenced by Waters et al. (2018b), reference benthic samples of *Anasterias* new to this study were collected from *Durvillaea* holdfasts on Chatham (Turanga (TU); 43°59'S, 176°39'E; Rebecca Cumming and Raisa Nikula), Campbell (Perseverance Harbour (PV); 52°33'S, 169°09'E); Northeast Harbour (NE); 52°31'S, 169°11'E; Elaine Leung), Auckland Islands (Ewing Island (EW); 50°31'S, 166°18'E); Enderby Island (EN) (50°30'S, 166°16'E; Raisa Nikula and Ceridwen Fraser), Bounty (Depot Island (DI) 47°45'S, 179°01'E; Raisa Nikula and Ceridwen Fraser), Crozet (Jardin Japonais, Possession Island (JJ) 46°21'S, 51°43'E; Sylvain Gutjahr) and Kerguelen (Port-Aux-Français (PAF); 49°21'S, 70°13'E Sébastien Mallol, Jean-Philippe Orts, David Renault and Marc Lebouvier) islands. Numbers after locality codes represent multiple occurrences of a haplotype at a single locality.

Figure S2: Examples of distinctive rafted rock clasts retrieved from the holdfasts of mainland-origin (STC1, A4) and sub-Antarctic-origin (A5) kelp rafts.

Figure S3: Ocean current and wind directions and speeds in the Southern Ocean near southwestern New Zealand for the inferred period (based on *Lepas*

barnacle lengths; Fig. 1b) of dispersal of kelp rafts from Fiordland and Snares Islands prior to beaching in southeastern New Zealand during the storm of 23 March 2018 (Fig. 1a). Data from <https://earth.nullschool.net>. Complex interactions of currents and winds in late February and early March may be responsible for the long transit times experienced by some rafts (Fig. 1b).

This material is available as part of the online article from <https://escholarship.org/uc/fb>

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