

Oceanic rafting by a coastal community

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Oceanic rafting is thought to play a fundamental role in assembling the biological communities of isolated coastal ecosystems. Direct observations of this key ecological and evolutionary process are, however, critically lacking. The importance of macroalgal rafting as a dispersal mechanism has remained uncertain, largely owing to lack of knowledge about the capacity of fauna to survive long voyages at sea and successfully make landfall and establish. Here, we directly document the rafting of a diverse assemblage of intertidal organisms across several hundred kilometres of open ocean, from the subantarctic to mainland New Zealand. Multispecies analyses using phylogeographic and ecological data indicate that 10 epifaunal invertebrate species rafted on six large bull kelp specimens for several weeks from the subantarctic Auckland and/or Snares Islands to the Otago coast of New Zealand, a minimum distance of some 400–600 km. These genetic data are the first to demonstrate that passive rafting can enable simultaneous trans-oceanic transport and landfall of numerous coastal taxa.

Keywords: dispersal; biogeography; macroalgae; drifting; invertebrate; marine

1. INTRODUCTION

Biologists have long speculated that passive rafting plays a fundamental role in assembling isolated (e.g. island) biotas [1–4], with the wide distributions of many ‘non-dispersive’ coastal species frequently accredited to this phenomenon [5]. Direct observations of rafting fauna, however, have been extremely rare [6–9], and the origins [7,8] and destinations [6,9] of rafts have remained largely speculative. Indeed, the importance of rafting is more typically invoked on the basis of observations of detached macroalgae and other flotsam at sea [10–20], or macroalgal fragments washed ashore [21,22]. Numerous studies have, additionally, inferred rafting dispersal on the basis of circumstantial evidence from biogeographic range data [10,23,24] or from evidence of genetic similarity among disjunct coastal populations [25–29]. Our genetic study is the first to explicitly demonstrate a trans-oceanic origin for rafted, beach-cast organisms.

The biotic communities associated with southern bull kelp provide a highly informative system for studies of trans-oceanic rafting. These isolated coastal benthic communities are linked primarily by the Antarctic Circumpolar Current (ACC, also known as the West Wind Drift), a strong, circumpolar current driven by prevailing westerly winds at subantarctic latitudes. Vast quantities of detached bull kelp have been observed floating in the path of the ACC [18], and apparently have potential to drift for long distances [11,18,21,28]. The holdfasts (basal attachment discs) of bull kelp are hollowed-out and occupied by diverse invertebrate taxa, which are consequently hypothesized to inherit some of the dispersal potential of their macroalgal host [5,18,29,30].

Six large specimens of detached southern bull kelp (*Durvillaea antarctica*), and their invertebrate passengers (molluscan, arthropod and echinoderm taxa), washed

ashore on St Clair Beach in mainland New Zealand in 2009–2010 (with five arriving in February 2009, and one in May 2010). We conducted genetic analyses of these bull kelp specimens, and of one of the invertebrate taxa associated with them, to determine the source population/s of the rafted communities.

2. METHODS

(a) Site and sample collection

Goose barnacles of the genus *Lepas* are pelagic, and only colonize floating objects at sea, such as driftwood or buoys [31,32]. Weekly inspection of beach-cast bull kelp (wrack) at St Clair Beach, South Island (New Zealand), typically reveals *D. antarctica* plants completely lacking or bearing only small goose barnacles (C. I. Fraser 2006–2010, personal observation; figure 1a), indicating a short duration at sea following local detachment [19]. By contrast, five complete specimens of beach-cast *D. antarctica* covered in notably large *Lepas australis* (figure 1b) were found at St Clair Beach on 26 February 2009, and a sixth such specimen was collected on 30 May 2010. Although numerous other bull kelp specimens were found on St Clair Beach on the sampling dates, only those with large (greater than 10 mm capitulum length) goose barnacles were collected.

Pieces of bull kelp frond tissue were preserved in 95 per cent ethanol in the field. Most of the bull kelp wrack specimens had multiple stipes but conjoined holdfasts (figure 1), indicating that each ‘specimen’ in fact comprised multiple bull kelp individuals. Whereas only one tissue sample was taken from each specimen for DNA analysis from the samples collected in February 2009 (wracks nos 1–5), a sample was taken from each of the four individuals that made up the specimen that arrived in May 2010 (wrack no. 6). Each bull kelp holdfast was placed in a plastic bag in the field and taken to the laboratory for dissection. Holdfasts were dissected using a large knife, with each cut into slices of approximately 20 mm width. Holdfast slices were inspected carefully by eye, and all

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Figure 1. Bull kelp wrack at St Clair Beach, New Zealand. (a) Photograph of a detached, beach-cast bull kelp specimen at St Clair Beach in March 2009 (not one of the rafts that formed the focus of this study). Bull kelp specimens are frequently deposited on St Clair Beach in southeastern New Zealand, but generally show no signs of lengthy oceanic drifting. For example, this specimen is estimated to have spent only a short period adrift, owing to complete absence of goose barnacles (*Lepas* sp.) that rapidly colonize buoyant objects at sea. (b) One of the six bull kelp wrack specimens of subantarctic origin. Encrustations of *Lepas* sp. of various sizes are visible on the holdfast and stipes of the bull kelp. (Photograph taken at St Clair Beach on 26 February 2009.) Scale bars, (a) 500 mm and (b) 50 mm.

invertebrates were removed using forceps and preserved in 95 per cent ethanol.

(b) Genetic analyses

DNA was extracted and partial sequences obtained for two genes for bull kelp: mitochondrial cytochrome c oxidase subunit I (COI) and chloroplast ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) following the protocols provided in Fraser *et al.* [33]. Partial mitochondrial COI sequences were obtained for *Limnoria* following the protocols provided in Nikula *et al.* [29]. Phylogenetic analyses of *D. antarctica* and *Limnoria* included previously published sequence data [28,29] as well as the wrack samples collected in 2009–2010. Sampling details of all attached bull kelp [28] and associated benthic invertebrate communities [29] are summarized in the electronic supplementary material, tables S1–S2. Published sequences of *Fucus vesiculosus* (GenBank accession no. AY494079) and congeneric taxa *Durvillaea potatorum* (FJ873092) and *Durvillaea willana* (EU918569) were included as outgroups in bull kelp analyses. Outgroup taxa used in the phylogenetic analysis of *Limnoria* were the isopods *Ligia hawaiiensis* (GenBank

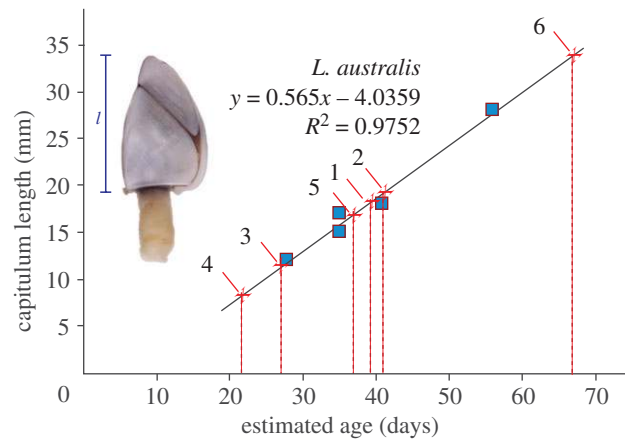


Figure 2. Estimation of goose barnacle age. Blue squares: estimated age plotted against capitulum length for *L. australis* in southeastern New Zealand waters, compiled using published data [31]. ‘Estimated age’ refers to the length of time floating beacons had spent adrift before collection and measurement of barnacles. Red crosses: capitulum lengths (l) of the largest *L. australis* from each of the six bull kelp wrack samples plotted against ages derived from the regression equation. The estimated age (in days) for each wrack specimen is: 67.7, 40.7, 39.2, 37.2, 27.1, 22.4. Wrack specimen identification numbers are shown. Upper-left image overlay, *L. australis* from bull kelp wrack (length approximately scaled to the y-axis).

accession no. AY051329) and *Mumma* sp. (GenBank accession no. HQ161066). Maximum likelihood (ML) phylogenetic trees were constructed using PHYML [34], applying the best-fit substitution model as determined by MODELTEST 3.06 [35] based on AIC (model parameters are given in electronic supplementary material, table S3). Robustness of the tree topologies was evaluated with 1000 replicate bootstrap analyses using PHYML [34], and with Bayesian posterior probability (PP) estimations in MRBAYES 3.1.2 [36] that used four MCMC chains of 5 000 000 generations, sampled trees each 100 generations and discarded the first 10 000 trees as burn-in. All unique DNA sequences determined during this study were deposited with GenBank (electronic supplementary material, table S1).

(c) Goose barnacle analyses

The duration of a macroalgal rafting event can potentially be estimated by analysis of the size of attached goose barnacles (*Lepas* sp.) that rapidly colonize flotsam in the marine environment [19,31,32,37]. For each bull kelp specimen, the 10 largest *Lepas* barnacles were removed and preserved in 95 per cent ethanol. Capitulum length of each *Lepas* was measured using digital vernier callipers following Hinojosa *et al.* [32]. The age of the largest barnacle from each bull kelp specimen—an indicator of minimum rafting duration—was estimated using published growth rates for *L. australis* in waters off New Zealand’s South Island [31] (figure 2).

3. RESULTS

(a) Genetic analyses

When compared with our Southern Hemisphere-wide genetic survey of *D. antarctica* [28], the mitochondrial (COI) and chloroplast (*rbcL*) DNA sequences of the beach-cast specimens show that the six bull kelp plants

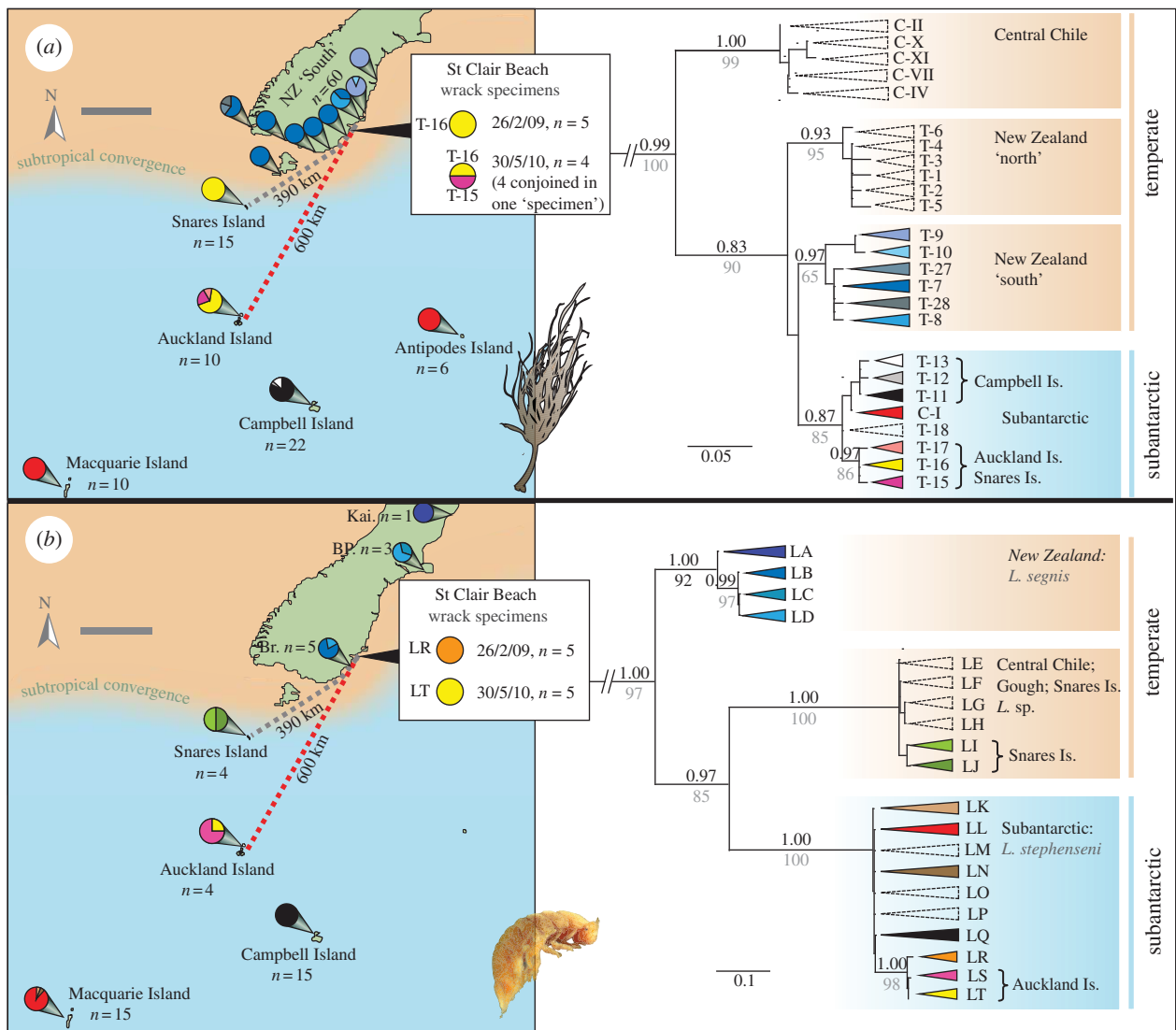


Figure 3. Genetic (mtDNA) evidence of a subantarctic source for beach-cast bull kelp specimens found on mainland New Zealand. (a,b): Left panels: map of the southern New Zealand region including subantarctic islands. Haplotype distributions and proportions for COI for (a) bull kelp, *D. antarctica*, and (b) the isopod *Limnoria* are shown as pie charts emerging from each site (site codes for mainland New Zealand: Kai, Kaikoura; BP, Banks Peninsula; Br, Brighton). Minimum-distance rafting trajectories from the Snares and the Auckland islands to St Clair Beach, New Zealand, are shown by dashed lines, with distances indicated. The approximate location of the subtropical convergence is shown. Right panels: phylogeographic relationships based on COI data for (a) bull kelp, *D. antarctica* and (b) the isopod *Limnoria*. Node support values of the major, well-supported branches are shown, with Bayesian PP values above and ML bootstrap values (in grey) below. Outgroups have been trimmed for clarity. Scale bars, (a,b) 200 km.

collected (those bearing large goose barnacles) all belong to an exclusively 'subantarctic' genetic lineage. This lineage is highly distinct from all mainland New Zealand lineages ([28,33]; figure 3 and electronic supplementary material, figure S1). More specifically, the COI haplotype shared by all six wrack specimens (haplotype T-16) has only been detected at two subantarctic island groups (Auckland Islands and Snares Islands [28]), and is distinct from haplotypes found at other subantarctic locations (including Campbell, Macquarie, Antipodes, Bounty, Kerguelen, Crozet, Marion, Gough and South Georgia islands). Of the four bull kelp individuals that comprised specimen no. 6 (collected in May 2010), two yielded the COI haplotype shared among the Snares and Auckland Islands, whereas two yielded a haplotype thus far only detected from the Auckland Islands (haplotype T-15 figure 3). Similar results were obtained for

chloroplast DNA, with three *rbcL* haplotypes detected among the six wrack specimens. One *rbcL* haplotype has previously been found only on the Snares and Auckland Islands (haplotype T-R-6; wrack specimen nos 1, 2 and 5), another only on the Auckland Islands (haplotype T-R-7; wrack specimen no. 6, all four individuals) and the third (haplotype T-R-15; wrack specimen nos 3 and 4) has not been previously detected but is closely related to the other two (electronic supplementary material, table S1 and figure S1).

In addition to information derived from the DNA analysis of the bull kelp wrack specimens themselves (above), their geographical origins may be elucidated by genetic characterization of associated epifaunal invertebrates. Several species from the isopod genus *Limnoria* are obligatorily algal-associated, and may spend their entire lives boring into macroalgal holdfasts [38–40].

Limnoria isopods secured from cavities of the wrack holdfasts (specimen nos 3, 5 and 6) were genetically highly divergent from all mainland New Zealand *Limnoria* haplotypes (*Limnoria segnis*), and instead grouped with the widespread subantarctic *Limnoria stephensi* (figure 3b). In particular, the mtDNA haplotypes of the rafted *Limnoria* were either identical or closely related to haplotypes that have only been detected from the Auckland Islands. All specimens of *Limnoria* collected from *D. antarctica* holdfasts from the Snares Islands, on the other hand, form a highly divergent mtDNA clade with specimens from central Chile and Gough Island (electronic supplementary material, table S1 and figure 3b: haplotypes LE–LJ).

Aside from the epifaunal *Limnoria* specimens and the abundant *Lepas* barnacles that colonize detached macroalgae via a planktonic larval phase [32], the bull kelp wrack specimens housed nine other macro-invertebrate taxa that were still alive upon landfall in New Zealand: one amphipod species (*Parawaldeckia karaka*); a pycnogonid (*Tanystylum antipodum*); six molluscan taxa (the bivalve *Kidderia* sp.; the gastropods *Cantharidus* ('*Margarella*') *rosea* and *Cellana strigilis*; the chitons *Onithochiton neglectus*—a brooder—and *Plaxiphora boydeni*; and the nudibranch *Fiona pinnata*); and an echinoderm (the rocky-reef sea-star *Stichaster australis*) (for abundance data, see electronic supplementary material, table S4). All of these taxa have distributions encompassing both southern mainland New Zealand and some of the New Zealand southern/subantarctic islands. All are benthic, with the exceptions of *L. australis* and *F. pinnata*, which colonize floating pelagic substrata. Preliminary genetic data (not shown) suggest there is no diagnostic mtDNA differentiation across the New Zealand subantarctic and mainland ranges of *C. rosea*, *O. neglectus* and *P. karaka*, making these taxa uninformative in determining geographical origins of beach-cast bull kelp specimens. The limpet *C. strigilis* was apparently a juvenile (shell length less than 2 mm), and was identified by comparison of an mtDNA (COI) sequence with sequences available on GenBank. Furthermore, this individual shared an identical 16S haplotype with specimens recently detected within bull kelp holdfasts from Campbell Island and in holdfasts of a large composite (*Macrocystis pyrifera* and *D. antarctica*) kelp raft drifting 13 km off Campbell Island (data not shown).

(b) Goose barnacle analyses

On the basis of capitulum growth rates derived from surveys of *L. australis* off eastern New Zealand (approximately 0.5 mm per day [31]), and the maximum size observed for *L. australis* on the beach-cast *D. antarctica* specimens, we infer that the five *D. antarctica* plants with the largest goose barnacles collected in February 2009 had spent a minimum of 20–40 days at sea before washing ashore, while the specimen collected in May 2010 had been at sea for at least 65 days. These estimates assume that colonization of drifting bull kelp by *Lepas* is as rapid on macroalgae as it was observed to be on the steel/wood beacons used in Skerman's [31] experimental study. Goose barnacles (*Lepas* sp.) are purely pelagic, colonizing drifting objects at sea [32], and have never, to our knowledge, been observed growing on attached bull kelp.

4. DISCUSSION

(a) Geographical origins of the rafts

Our genetic analyses of beach-cast bull kelp (*D. antarctica*) and their isopod (*L. stephensi*) passengers show that the wrack specimens recovered from St Clair Beach in February 2009 and May 2010 were undoubtedly of subantarctic origin, and had drifted at least 390 km (from the Snares Islands) or 600 km (from the Auckland Islands). The strong buoyancy of *D. antarctica* means that wind, in addition to water movement, is likely to play a major role in determining the geographical fate of drifting specimens [41–43]. Although southern New Zealand is broadly dominated by westerly winds [44], summer months can be marked by prevailing easterlies that periodically deposit macroalgae onto the eastern shores of the South Island [45], as during mid to late February 2009 (electronic supplementary material, figure S2). Indeed, a recent oceanographic modelling study based on empirical data from satellite drifters [46] showed that buoyant objects originating from the Auckland and Snares Islands are likely to be driven northwards to arrive on New Zealand mainland shores. By contrast, the same study showed that drifters from other subantarctic sources (e.g. Campbell, Antipodes, Bounty and Chatham islands) tend to be driven away from New Zealand [46]. Genetic data from bull kelp specimen no. 6 strongly suggest the Auckland Islands as its source (two COI and four *rbcL* haplotypes from specimen no. 6 were previously detected only from the Auckland Islands). Furthermore, data from *L. stephensi* collected from three of the beach-cast specimens (nos 3, 5 and 6) also promote the Auckland Islands as the most likely source population. Bull kelp holdfasts around New Zealand's South Island are inhabited by *L. segnis*, whereas subantarctic bull kelp populations primarily host *L. stephensi* [39,29]; the former species has been recorded only from New Zealand, and the latter only from the subantarctic region [38]. Despite being common across the subantarctic, *L. stephensi* has never been recorded from the Snares Islands, although several other species of algal-associated *Limnoria* have [38]. The epifaunal genetic data are therefore compatible with wrack specimens nos 3, 5 and 6 originating from the Auckland Islands. In contrast, the sea-star *S. australis* has previously been recorded from the Snares Islands [47], but not yet from the Auckland Islands. At least one of the wrack specimens may, therefore, have originated from the Snares Islands. Buoyant material has a tendency to accumulate in 'windrows' (along the lines formed by near-surface oceanographic features called Langmuir cells [48]) and drifting macroalgae from different origins may therefore meet at sea and become entangled, continuing the journey together to arrive at a common destination. We propose that the beach-cast bull kelp specimens that form the focus of this study originated from both the Snares and Auckland Islands, and were driven by wind and oceanographic features to arrive at St Clair Beach roughly simultaneously.

(b) Speed of travel

The maximum sizes of goose barnacles (*L. australis*) attached to the bull kelp wrack indicate a drifting duration of at least 20–40 days for the specimens collected in

February 2009, and at least 65 days for the specimens collected in May 2010. If the bull kelp wrack specimens carrying the smaller *Lepas* (estimated to be about 20 days old) originated from the closest possible source (the Snares Islands), and if they travelled in a direct line from origin to destination, they must have drifted at an average speed of about 0.2 m s^{-1} . Alternatively, if these bull kelp specimens originated from the Auckland Islands, their average speed must have exceeded 0.3 m s^{-1} . With neither currents nor wind likely to have driven them directly from origin to destination, the drifting bull kelp would almost certainly have travelled considerably greater distances than the minimum, straight-line trajectories shown in figure 3, and at much greater speeds than those estimated above. Regardless, the speeds and durations of these inferred rafting events are consistent with a recent oceanographic modelling study which indicates that passively drifting objects originating from the Auckland Islands can reach south-eastern South Island within 30–50 days of departure [46]. A study by Coombs and Landis [49] showed that pumice from a volcanic eruption in the South Sandwich Islands (east of the southern tip of South America) began to wash up on New Zealand shores 530 days after the eruption, and must therefore have travelled at a speed of around 0.3 m s^{-1} . Similarly, a review of records of drifting objects at sea by Thiel and Gutow [42] concluded that most travel at an average speed of approximately $0.1\text{--}0.3 \text{ m s}^{-1}$. The longest distance between any two land masses with *D. antarctica* populations in the path of the ACC is approximately 8000 km, from New Zealand to the southern tip of South America. With drifting *D. antarctica* clearly able to travel at a comparable speed to the pumice noted by Coombs and Landis [49], detached bull kelp could potentially traverse the distance between, for example, New Zealand and South America in a little under a year, or the distance between Gough Island (Atlantic Ocean) and the Kerguelen Islands (Indian Ocean) in three or four months. Such durations may well be within the lifespans of their invertebrate passengers, and/or subsequent generations of those that brood their offspring within the bull kelp holdfasts (e.g. *Limnoria* [40]).

(c) Rafting realized

The ecological and evolutionary importance of macroalgal rafting as a dispersal mechanism has long remained uncertain, largely owing to lack of knowledge regarding the capacity of fauna to: (i) survive long voyages at sea and (ii) successfully make landfall and establish [5,18]. Recent research has demonstrated that, in spite of faunal abundance dropping sharply in macroalgal holdfasts within minutes of detachment, there is little change in the number of passengers during subsequent hours, indicating a high rafting potential of those that remain [50,51]. The level of epifaunal diversity we detected in the bull kelp wrack specimens parallels that observed in an experimental epifaunal study of artificially detached, moored *D. antarctica* [30], and shows that successful long-distance transportation is indeed possible for a broad suite of algal-associated marine invertebrate taxa.

Our results demonstrate survival of numerous taxa during the rafting journey and following landfall, but successful colonization of a new territory also relies on establishment of immigrants in their new environment. Negligible mtDNA differentiation between subantarctic and mainland populations of the bull kelp-associated taxa *C. rosea*, *O. neglectus* and *P. karaka* (of which the latter two are brooders) suggests that rafting may indeed facilitate dispersal of these taxa. Similarly, the wide (subantarctic and mainland) distribution of the brooding pycnogonid *T. antipodum* [52] and of the chiton *P. boydeni* [53] suggests these species may also use bull kelp for long-distance dispersal and migration. A recent phylogeographic study of the limpet *C. strigilis* showed low mtDNA diversity among sites in southern New Zealand and the New Zealand subantarctic [54]. Our discovery of a juvenile *C. strigilis* on wrack specimen no. 6, as well as numerous juveniles on bull kelp drifting offshore close to Campbell Island, and within bull kelp holdfasts at Campbell Island, suggests that drifting bull kelp may facilitate population connectivity of this species. Conversely, the absence of subantarctic *Limnoria* and *Durvillaea* genetic lineages around mainland New Zealand implies that establishment of new immigrants of these taxa can be limited by extrinsic factors, such as temperature, or by the presence of pre-existing conspecific or congeneric populations [28]. Success also necessarily depends on landfall being made at a suitable location; invertebrates from the six rafts studied here, for example, would have been unlikely to survive, as they were deposited on a sandy beach rather than rocky shore habitat. Broadly, however, our study demonstrates an important ecological mechanism that is likely to have facilitated the post-glacial recolonization of subantarctic coasts following the Last Glacial Maximum [28,29].

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