

Cyclone-driven marine rafting: storms drive rapid dispersal of buoyant kelp rafts

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ABSTRACT: Storm events can have strong effects on marine biological dispersal. Here, we used geological evidence to assess the speed of biological rafting driven by a major cyclonic storm (Cyclone Gita) in southern New Zealand during February 2018. We undertook a comparative analysis of coastal rock types to assign beach-cast macroalgal specimens to their geological source regions. Approximately 10% (23 of 250) of *Lepas*-encrusted beach-cast kelp (*Durvillaea*) specimens sampled from Dunedin beaches in the immediate aftermath of Cyclone Gita (22 and 23 February 2018) bore holdfast-clasts consistent with origins in the distant Fiordland region of southwestern South Island. Based on *Lepas* barnacle growth data, we estimated that this distinctive 'pulse' of rafted material achieved the 350 to 500 km journey from Fiordland to Dunedin in as little as 10 d, with many of these rafts thus inferred to have travelled 30 to 50 km d⁻¹. These rapid rafting events were facilitated by westerly gales in Foveaux Strait (12 to 17 February), followed by cyclonic southeasterly winds off eastern South Island (19 to 21 February). The rafting-speed estimates from this study are substantially faster than mean current-flow estimates for the same coastal region (12 to 20 km d⁻¹), and also exceed the speeds of previously documented kelp-rafting events in this region (estimated 10 to 15 km d⁻¹) and elsewhere. Together, these data highlight the key role of storms in driving 'wind slippage' of buoyant material, facilitating pulses of dispersal at speeds far exceeding the predictions of oceanographic models.

KEY WORDS: Dispersal · Geology · Oceanography · Rafting · Storm · Wind slippage

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INTRODUCTION

Ocean scientists have long sought to understand how physical processes govern biological assemblages (e.g. Ali & Huber 2010). While prevailing oceanographic features can give rise to predictable patterns of species disjunction (Briggs 1974, Gaylord & Gaines 2000) and repeated sites of population genetic turnover (White et al. 2010, Bussolini & Waters 2015), more sporadic physical events can also have substantial biological implications (e.g. Carlton et al. 2017). In particular, it is thought that storm events can influence biology by facilitating dramatic cases of long-distance dispersal (e.g. Censky et al. 1998, Monzón-Argüello et al. 2012, Fraser et al. 2018).

Indeed, recent studies have suggested that storm-driven dispersal events can have major effects on both biogeography and ecosystem assembly (Gillespie et al. 2012). Despite increasing recognition of storm-forced dispersal as a potentially important process, however, little is understood about the timeframes required (and biological plausibility) of such events.

Passive rafting on macroalgal substrata is likely to be an important biogeographic mechanism for numerous marine epibiotic species that lack autonomous dispersal potential (Thiel & Haye 2006). Widespread buoyant kelps of the southern genus *Durvillaea* harbor diverse epibiotic communities (Fraser et al. 2011) and thus present ideal systems for addressing rafting-mediated dispersal in cool-temperate oceans of

the Southern Hemisphere. Recent molecular studies have inferred that kelp rafting is an important driver of transoceanic marine connectivity in the south Pacific Ocean (Nikula et al. 2010, Cumming et al. 2014). Additionally, observations at sea indicate that buoyant *Durvillaea* can drift for substantial distances in the Southern Ocean (Smith 2002, Fraser et al. 2017). Despite ever-improving surface oceanographic models, however, the extent to which strong winds can enhance the rafting speed of strongly buoyant objects ('wind slippage') remains poorly understood.

Recent studies have started to address the dynamics of marine biological rafting by combining biological and physical data sets. Emerging data from the New Zealand region, for instance, suggest that temporal variation in wind conditions can play a major role in constraining the dispersal dynamics of rafting macroalgae (Garden et al. 2011, 2014). Indeed, recent studies have detected cases of long-distance (>1000 km) transoceanic dispersal driven by major storm events (Fraser et al. 2011, Waters et al. 2018). However, the speed of such storm-driven rafting events has yet to be well quantified.

Here, we documented a distinctive pulse of fast-dispersing kelp material driven ashore by a major cyclonic storm, Cyclone Gita, in southern New Zealand on 20 and 21 February 2018 (see Figs. 1 & 2). We used a combination of biological and geological analyses to pinpoint the source regions of rafted kelp and rock specimens and to estimate the timeframe of rafting journeys. By quantifying the speed of storm-driven rafting events, we shed new light on the rapidity by which wind-blown buoyant material can disperse at sea.

MATERIALS AND METHODS

Fieldwork

Cyclone Gita was a major storm that impacted much of the southwest Pacific Ocean in February 2018, ultimately reaching southern New Zealand on 20 and 21 February (see Fig. 1). Strong southeasterly winds affected coastal regions

across eastern South Island during this period (wind data retrieved from <http://earth.nullschool.net> for Fig. 1, and <http://cliflo.niwa.co.nz> for Figs. 1 & 2). In the aftermath of the cyclone, samples of beach-cast *Durvillaea* (see Fig. 5a), with associated epibiota and geological clasts, were collected from 4 beaches at the city of Dunedin (Victory Beach: 45° 50' S, 170° 44' E; Allans Beach: 45° 52' S, 170° 42' E; St. Clair: 45° 54' S, 170° 30' E; Brighton: 45° 56' S, 170° 20' E; see Fig. 1a, Table 1). Specifically, kelp sampling was conducted within 1 to 48 h of the cessation of strong onshore winds in Dunedin (22 and 23 February 2018). The storm led to deposition of a clearly identifiable 'cohort' of newly beach-cast kelp material, most of it (250 of approximately 350 *Durvillaea* specimens inspected) covered by *Lepas australis* (see Fig. 5b), an obligate rafting barnacle species that colonises only substrata adrift at sea. Sampled kelp specimens were considered to be freshly beach-cast if they had live epibiota and were non-desiccated. To avoid sampling 'local' kelp specimens (e.g. detached from immediately adjacent rocky shores), we collec-

Table 1. Geological and biological details of 23 beach-cast *Durvillaea* specimens collected from Dunedin beaches (22 and 23 February 2018) yielding holdfast rocks consistent with Fiordland origins (>350 km by sea from the collection localities). The range of capitulum lengths (mm) for the 3 largest *Lepas australis* barnacles collected from each specimen is given, together with the estimated floating durations (days) based on the largest barnacle observed. The 4 samples in **bold** are unambiguously of Fiordland origin. Sample codes: A: Allans Beach; V: Victory Beach; S: St. Clair Beach; B: Brighton Beach

Sample	<i>Lepas</i> (mm)	Duration (d)	Holdfast rock	Geological origin
A1	3.9–4.4	14.9	Biotite granitoid schist/gneiss	Fiordland / Stewart Is
V1	2.1–2.3	11.2	Hornblende-biotite granitoid	Fiordland / Stewart Is
V9	3.0–3.2	12.8	Hornblende-biotite granitoid	Fiordland / Stewart Is
S1	2.1–2.3	11.2	Granitoid	Fiordland / Stewart Is
S26	2.3–2.8	12.1	Hornblende-biotite granitoid	Fiordland / Stewart Is
S30	6.8–7.6	20.6	Granitoid	Fiordland / Stewart Is
S31	2.6–3.2	12.8	Granitoid	Fiordland / Stewart Is
S33	1.8	10.3	Hornblende granitoid	Fiordland / Stewart Is
S34	2.1	10.9	Hornblende granitoid	Fiordland / Stewart Is
S38	1.9–2.1	10.9	Granodiorite	Fiordland / Stewart Is
S39	2.0–2.3	11.2	Hornblende-biotite, micro-granitoid	Fiordland / Stewart Is
S40	2.0–2.4	11.4	Granitoid	Fiordland / Stewart Is
S42	6.5–7.2	19.9	Granitoid	Fiordland / Stewart Is
S44	2.6–3.0	12.5	Granitoid	Fiordland / Stewart Is
S46	2.0–2.1	10.9	Hornblende-biotite micro-granitoid	Fiordland / Stewart Is
S47	2.2–2.4	11.4	Granitoid	Fiordland / Stewart Is
S57	4.9–5.3	16.5	Granitoid	Fiordland / Stewart Is
S58	2.6–3.0	12.5	Granitoid	Fiordland / Stewart Is
B3	1.9–2.0	10.7	Hornblende-biotite granitoid	Fiordland / Stewart Is
S60	2.0–2.1	10.9	Feldspathic garnet amphibolite	Fiordland
S32	1.9–2.0	10.7	Garnet hornblende gneiss	Fiordland
S36	2.5–2.7	11.9	Muscovite biotite pelitic gneiss	Fiordland
S4	2.7–3.0	12.5	Calcareous sandstone	Fiordland

ted only kelp specimens covered in *L. australis*. For each specimen, we sampled *Durvillaea* frond tissue, together with the largest *L. australis* specimens present, along with other holdfast epifauna and attached rock material. All samples were stored in labelled plastic bags and returned to the laboratory, where they were stored frozen prior to analysis.

Geological analysis

Rocks were found attached to holdfasts of 40 of the 250 *L. australis*-covered *Durvillaea* specimens inspected in the aftermath of Cyclone Gita. These rocks ranged in size from mm-scale veneers up to 0.4 kg. Mineral content, textures and identifications of rocks were determined by standard petrographic microscopic observations, including polished thin sections. Rock samples and sections are available by request from the Geology Department, University of Otago. The rocks were compared to the regional coastal geology of southern New Zealand and the subantarctic islands (see Fig. 3, Table 2), to determine probable coastal source areas. An extensive archive of rocks from these various localities is stored in the Geology Department, University of Otago, and these archival rocks, along with the personal experience of the second author, were used for locating probable coastal source areas for the kelp-rafted rocks. Rock descriptions and locations for *in situ* specimens in the archive are available online via the Petlab database (Strong et al. 2016) hosted by GNS Science, New Zealand (<https://pet.gns.cri.nz/#/>). See Table 2 for distinctive features and minerals of the key rock units used in these comparisons to kelp-rafted rocks. Further geological information on rafted rocks and their probable sources is presented in Craw & Waters (2018).

Biological analysis

For each bull-kelp specimen (e.g. see Fig. 5a), the maximum size of attached *L. australis* barnacles (see Fig. 5b) was used to estimate rafting duration. These calculations used size/age data for *L. australis* from Skerman (1958) for southern New Zealand waters, in temperatures (up to 16°C) comparable to those of southeast New Zealand waters during February 2018. *L. australis* capitulum length was measured using digital calipers, and time adrift at sea was estimated using the regression: $y = 0.565x - 4.0359$ (y = maximum capitulum length; x = days) after Fraser et

al. (2011). Although there may be some regional variation in the rates at which *L. australis* colonises and grows on buoyant substrata, previous studies have indicated tight relationships between *L. australis* maximum capitulum length and time at sea (Skerman 1958, Fraser et al. 2011; $R^2 = 0.98$); and between *L. australis* size and journey distance (e.g. transoceanic versus local; Waters et al. 2018). Overall, therefore, it seems clear that *L. australis* size provides a useful proxy for relative time adrift at sea.

RESULTS

Onset of Cyclone Gita

Southern New Zealand experienced a large amount of cyclonic activity in January and February 2018. First, Cyclone Fehi arrived in late January, and passed right across the country and affected even the southern South Island on 1 February. This event was quickly followed by Cyclone Gita in mid-late February. The aftermath of Cyclone Fehi and onset of Cyclone Gita in southern New Zealand was preceded by a period of strong westerly winds (Fig. 1a,b). These westerly winds were particularly persistent around the southern portion of the South Island (Fig. 1a,b), as recorded at Tiwai Point weather station in Foveaux Strait (Figs. 2 & 3). Wind speeds of 30 to 50 km h⁻¹ predominated, with gusts up to 80 km h⁻¹ (Fig. 2). As the cyclone moved south, the westerly winds rapidly gave way to strong easterly winds near the southeast corner of the South Island, resulting in strong onshore winds along the eastern coast (Figs. 1c,d & 3). The eastern coast near Dunedin city, the region from which samples were collected for the present study (see above), received consistent easterly winds of 20 to 40 km h⁻¹ for most of 21 February (Fig. 1d).

Rafted rocks and their sources

A total of 250 *Lepas*-covered *Durvillaea* holdfasts were inspected, 40 (16%) of which yielded rock material attached to the holdfasts. Some of the holdfast rocks (14) were derived from nearby geological sources (Fig. 3, Table 2). Seven of these rocks were Dunedin basalt, derived <20 km from collection locality, and 7 rocks were Otago schist derived from <60 km to the south (Fig. 3, Table 2). A further 3 rocks were Murihiku terrane metagreywacke clasts sourced from the Catlins region of southeastern

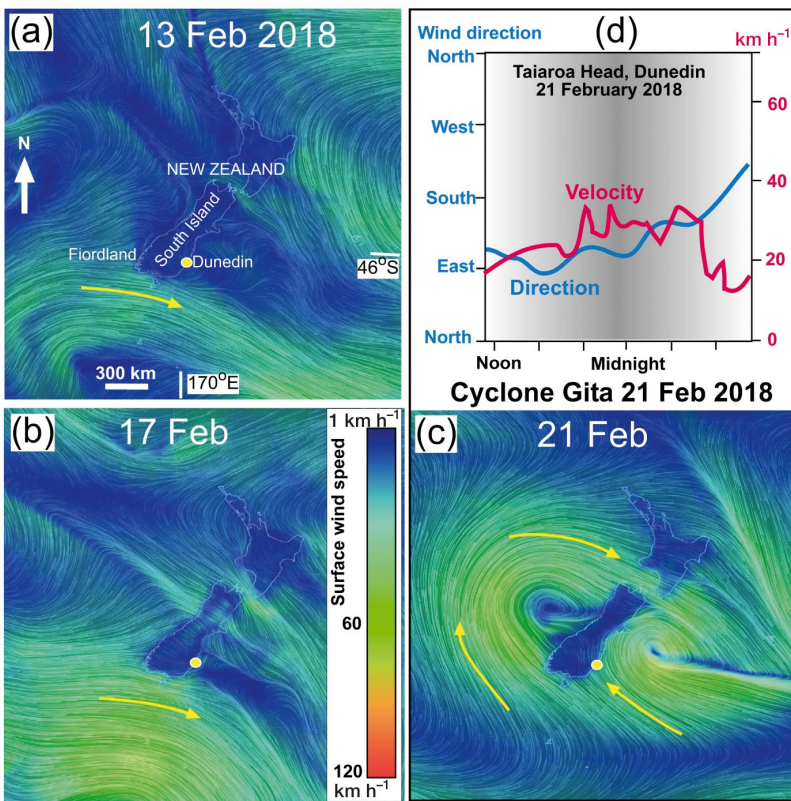


Fig. 1. Southern New Zealand, with a summary of meteorological events driving dispersal of Fiordland kelp specimens to Dunedin in February 2018. Wind data from <http://earth.nullschool.net>. (a,b) Strong westerly winds drove rapid eastward dispersal of kelp rafts through Foveaux Strait (13 to 17 February) prior to the arrival of (c,d) Cyclone Gita, which facilitated northeasterly dispersal onshore to Dunedin beaches

South Island (<170 km south of collection locality; Fig. 3, Table 2). In contrast, 4 rock-bearing specimens (a biotite gneiss, 2 garnet amphibolite gneisses, and 1 calcareous sandstone) were clearly derived from the far more remote (350 to 500 km distant) coastal region of Fiordland (Fig. 3, Table 1), based on geological features outlined in Table 2. An additional 19 specimens yielded granitoid clasts that must have come from either Fiordland (>300 km) or, alternatively, at least 230 km from the Stewart Island and Foveaux Strait region (Fig. 3, Table 2). The key features used for distinguishing locally derived rocks from rocks that dispersed substantially further were the mineral grain sizes and the presence or absence of the distinctive minerals biotite, muscovite, garnet and hornblende (Table 2, Fig. 4a,b). Coarse grain size (commonly mm scale) of muscovite and biotite was also indicative of a distant, rather than local, origin of these rocks.

Cenozoic sandstones deposited on older basement in southern New Zealand contain fragments of the basement from which they were

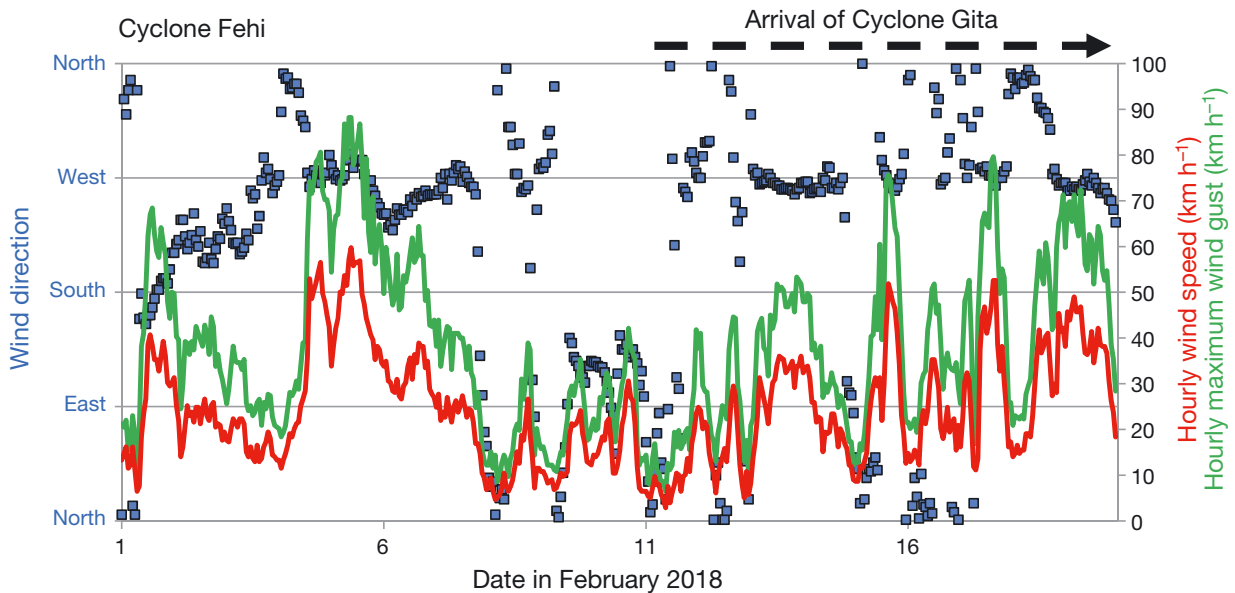


Fig. 2. Wind strength and direction in Foveaux Strait in southern New Zealand (Tiwai Point; see Fig. 3 for location) during the arrival of Cyclone Gita in February 2018. Data from <http://cliflo.niwa.co.nz>

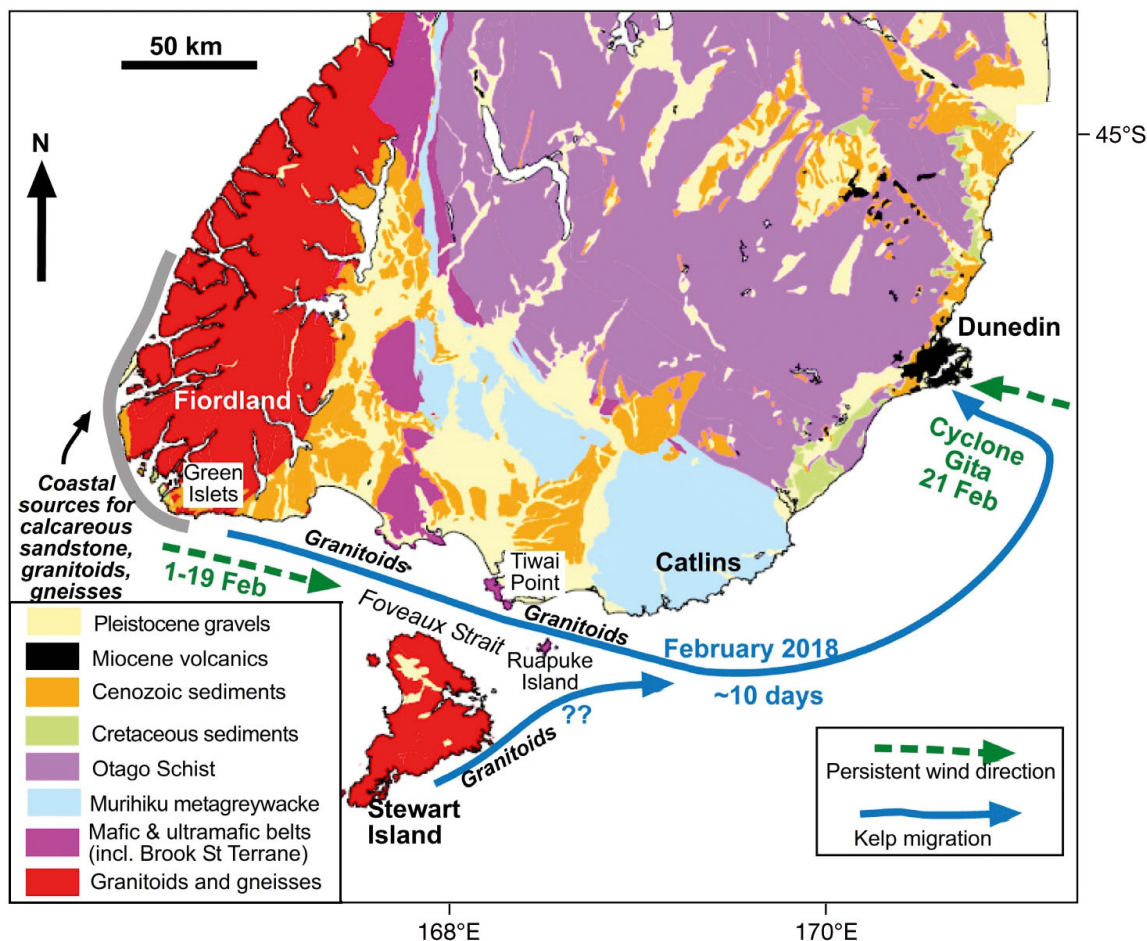


Fig. 3. Geological map of southern New Zealand, illustrating major rock groupings used to establish geographic sources of rafted *Durvillaea* specimens, and the inferred long-distance migration pathway(s) of rock-bearing kelp. Distinctive Fiordland rocks are inferred to have been derived from the indicated grey coastal zone, and less-distinctive granitoids may have been derived from a range of localities in the Fiordland and Foveaux Strait area

Table 2. Distinctive minerals in rock units exposed on southern New Zealand coastline (see Fig. 3), used to assign beach-cast kelp to geological source regions

Rock unit	Typical mineral grain size	Muscovite	Biotite	Red garnet	Hornblende
Dunedin volcanics	< 50 μm ; basalts	Absent	Absent	Absent	Rare
East coast Cenozoic calcareous sandstone	< 50 μm ; Otago schist-derived	Abundant, fresh, < 50 μm	Absent	Absent	Absent
Otago schist	< 100 μm	Abundant, fresh, < 100 μm	Very rare, < 20 μm , altered	Absent	Absent
Murihiku Terrane	< 50 μm	Abundant, altered, < 50 μm	Rare, altered	Absent	Rare, altered
Brook St. Terrane	Up to 2 mm	Absent	Fresh, in granitoids	Absent	Fresh, in granitoids
Fiordland basement	Up to 2 mm	Minor in granitoids, gneisses; fresh, up to 2 mm	Fresh, in granitoids, gneisses	Abundant in gneisses, amphibolites	Abundant in granitoids, amphibolites
Fiordland Cenozoic calcareous sandstone	Up to 1 mm; granitoid- and gneiss-derived	Minor, fresh, up to 1 mm	Abundant, fresh, up to 1 mm	Minor	Abundant, fresh, up to 1 mm

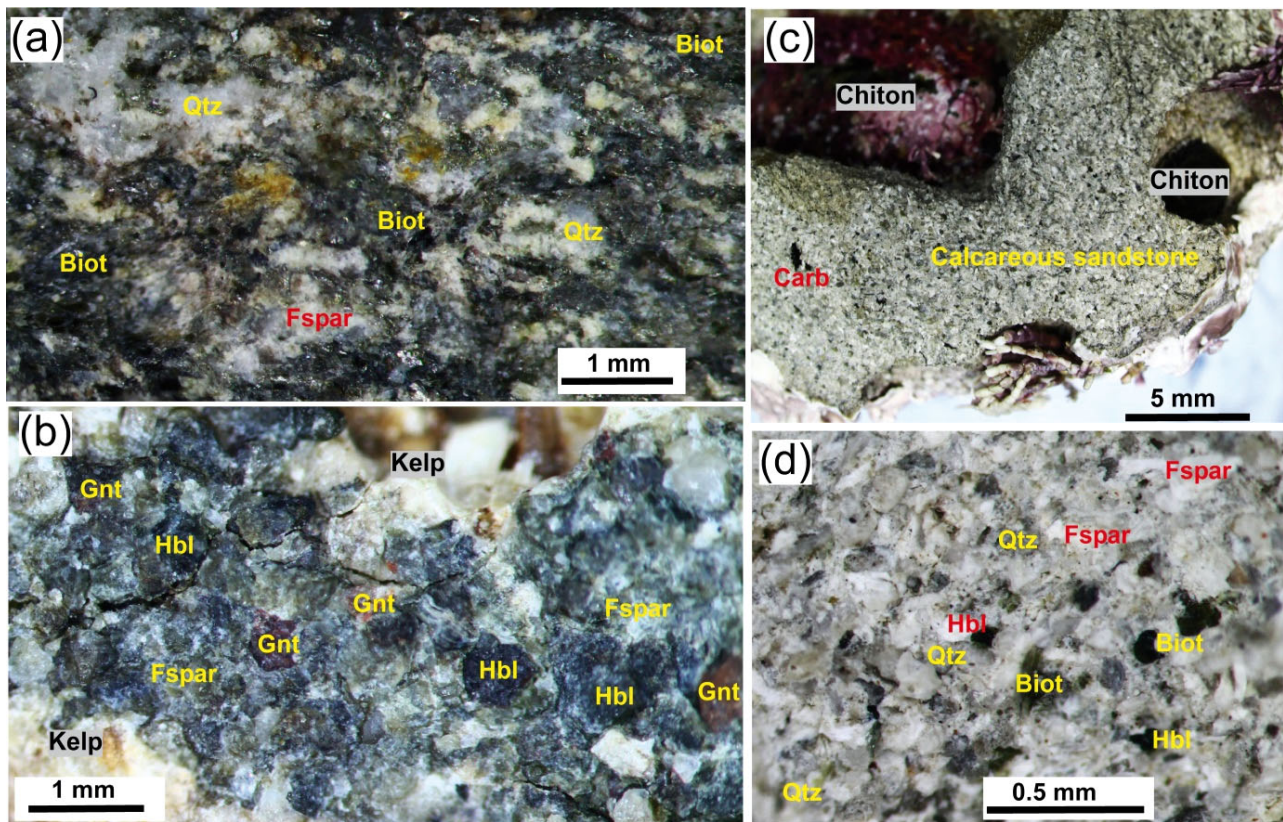


Fig. 4. Distinctive kelp-rafted rocks from southwestern Fiordland (see Fig. 3), collected from *Durvillaea* holdfasts on Dunedin beaches on 22 and 23 February 2018. (a) Coarse-grained biotite gneiss; (b) garnet (Gnt) amphibolite gneiss veneer on a kelp holdfast; (c,d) calcareous sandstone with angular granitoid-derived minerals quartz (Qtz), feldspar (Fspar), biotite (Biot) and hornblende (Hbl), and minor carbonaceous material (Carb). Associated rafted epibiota include coralline algae and chitons

derived, and the marine sediments are commonly cemented with calcite. Hence, Cenozoic calcareous sandstones along the eastern coast near Dunedin (Fig. 3) were derived from the Otago schist, and the minerals within the sandstones—notably the absence of biotite and hornblende—reflect that origin (Table 2). In contrast, Cenozoic calcareous sandstones resting on Fiordland basement, the other set of Cenozoic rocks on the southern New Zealand coastline (Fig. 3; Carter & Lindqvist 1975), are dominated by minerals and rock fragments derived from the granitoids and gneisses of the nearby Fiordland basement, with distinctive coarse grained biotite and hornblende clasts that are not found in sandstones derived from Otago schist (Table 2). Because of these clear regional distinctions between sandstone mineral contents, it is possible to readily distinguish the sources of kelp-rafted calcareous sandstones that arrived on Dunedin beaches. The calcareous sandstone collected from a St. Clair Beach specimen (Fig. 4c,d) is one of the most distinctive of all the sam-

ples collected for this reason. The sand clasts in the rock were derived from granitoid basement sources, yielding abundant angular labile minerals including feldspar, biotite and hornblende (Fig. 4c,d). The rock also contained minor amounts of carbonaceous material (Fig. 4c). All these features confirm that this rock is a close match to rocks from the southwestern corner of Fiordland, to the west of Green Islets (Fig. 3; Carter & Lindqvist 1975, Turnbull et al. 2010), and must therefore have travelled at least 350 km to the Dunedin coast.

Rafting duration

The size of epibiotic *Lepas australis* barnacles provides a useful proxy for estimating a raft's time adrift at sea. Based on size/age data for *L. australis* previously documented by Skerman (1958) (see Fraser et al. 2011), we estimate that many of the rafting events from Fiordland to Dunedin were completed in less



Fig. 5. (a) Beach-cast *Durvillaea antarctica* (specimen S1 in Table 1) at St. Clair Beach, Dunedin, in the aftermath of Cyclone Gita, 22 February 2018 (holdfast diameter 15 cm). (b) Granitic holdfast veneer indicates a distant origin (Stewart Island or Fiordland) for this rafted specimen, and the small attached *Lepas australis* barnacles (<3.0 mm), suggest a short rafting timeframe (<12 d)

than 2 wk. Specifically, the 4 beach-cast *Durvillaea* specimens (e.g. Fig. 5a) containing rocks definitively of Fiordland origin all yielded consistently small *L. australis* barnacles (maximum capitulum lengths 2.0, 2.1, 2.7 and 3.0 mm, respectively; Fig. 5b), indicating approximate rafting durations of 10 to 12 d. Similarly, the 19 beach-cast *Durvillaea* specimens containing granitic clasts (indicating Stewart Island or Fiordland origins; Table 1) yielded an average maximum *L. australis* capitulum length of 3.2 mm (range 1.8 to 7.2 mm; 15 of 19 specimens with *L. australis* <4 mm), or an average duration estimate of 13 d. Together, these time estimates suggest dispersal speeds exceeding 30 km d⁻¹ and perhaps as high as 50 km d⁻¹ (see below).

DISCUSSION

In the present study we documented an anomalous 'pulse' of Fiordland-origin kelp rafts driven ashore by a major cyclonic storm, Cyclone Gita, in southern New Zealand in early 2018. The majority (~70%) of beach-cast specimens inspected in the aftermath of this event were covered in *Lepas australis* barnacles, suggesting non-local origins, and this inference was further reinforced by the finding that most (23 of 40) of the rock-bearing specimens were derived from geological sources several hundred kilometres away. The size distribution of *Lepas* barnacles detected on beach-cast *Durvillaea* material in the aftermath of Cyclone Gita was notably narrower than for previous storms from the same region (e.g. Fraser et al. 2011, Waters et al. 2018). Despite the detection of a few specimens with large barnacles (>7 mm), the vast majority of putative Fiordland-origin specimens yielded small *L. australis* with capitulum lengths in the range of 2 to 4 mm (Table 1). The proportion of holdfast geological clasts with putative Fiordland origins (up to approximately 60% of rock specimens collected) also substantially exceeded proportions found in previous geological studies (Garden et al. 2011, Waters & Craw 2017, Waters et al. 2018), where Fiordland-origin specimens comprised only small proportions (1 to 2%) of total samples. Together, these data suggest that the unique combination of wind and oceanographic conditions in early-mid February 2018 (Figs. 1–3) facilitated rapid dispersal of a distinctive 'cohort' of kelp rafts between Fiordland and Dunedin.

The majority of putatively Fiordland-origin specimens are estimated to have come from geological sources in southwestern Fiordland, some 350 to 500 km by sea from the Dunedin beaches where they were ultimately deposited and sampled (Fig. 3). Given the estimated 10 to 13 d rafting durations, we suggest the rafts were detached from the Fiordland coast around 9 to 12 February 2018. The consistent westerly winds (Figs. 1a,b, 2 & 3) likely drove the rapid eastward dispersal of these *Durvillaea* rafts through Foveaux Strait. Subsequently, the arrival of Cyclone Gita (21–22 February) produced southeasterly winds, driving the rafting specimens northwards and onshore to Dunedin beaches on 22 February (Figs. 1c,d & 3).

The 350 to 500 km rafting journey of numerous specimens from Fiordland to Dunedin, over an approximately 10 to 13 d window, suggests average travel speeds of around 30 to 50 km d⁻¹. These rafting speed estimates are considerably higher than mean

current-flow estimates for the same coastal region (12 to 20 km d⁻¹; Chiswell 1996). They also substantially exceed the velocity estimates of previously documented *Durvillaea* rafting events in southern New Zealand (10 to 15 km d⁻¹; Waters & Craw 2017; 6 km d⁻¹; Hawes et al. 2017) and the subantarctic (17 to 26 km d⁻¹; Fraser et al. 2011). Similarly, Harrold & Lisin (1989) monitored drifting of giant kelp *Macrocystis pyrifera*, finding that the vast majority of specimens travelled slower than 0.15 m s⁻¹ (<12 km d⁻¹) (although one specimen achieved the unusually fast speed of 0.65 m s⁻¹). Subsequent *Macrocystis* rafting studies by Hobday (2000) and Hernandez-Carmona et al. (2006) have yielded similarly slow rafting velocities (7 to 9 km d⁻¹). Speed estimates from the present study also exceed rafting velocities documented for other buoyant biological material. For instance, Censky et al. (1998) inferred that rafts of trees uprooted by hurricanes traversed the 250 km sea gap between Guadeloupe and Anguilla in approximately 3 wk (i.e. around 12 km d⁻¹). Broadly, most direct measurements of drifting objects at sea report velocities of less than 1 km h⁻¹ (<24 km d⁻¹), albeit with occasional notable exceptions (see Table 8 in Thiel & Gutow 2005). Given this context, the rapid velocity estimates from the present study suggest that strong winds have the potential to drive rafting dispersal at speeds far exceeding those expected under prevailing oceanographic and meteorological conditions.

Oceanographers have long sought to understand and model the physical parameters likely to affect marine biological processes (e.g. Chiswell et al. 2003, Ali & Huber 2010, Fraser et al. 2018). Prevailing oceanographic data can often provide a strong framework for predicting rafting dispersal directions (e.g. Collins et al. 2010, Garden et al. 2014). Indeed, in the present study we found no evidence of rafts having dispersed against prevailing oceanographic currents (e.g. from geological sources north of Dunedin). Despite ever-improving oceanographic models for the world's oceans, however, comparatively little is known about the extent to which wind can increase rafting speed of buoyant drifting material relative to the speed of surface currents themselves. In a recent study, Rio (2012) analysed dispersal in buoys at the ocean surface in the Antarctic Circumpolar Current and concluded that 'wind slippage' can increase velocity of such drifters by as much 0.13 m s⁻¹ (11 km d⁻¹), in contrast to results of previous analyses (e.g. Poulain et al. 2009). Similarly, Krauss et al. (1989, p. 3201) noted that drifters at the surface 'are strongly affected by wind and cannot be used for the analysis of currents without correction, even under light

winds'. These findings are supported by the results of the present study, which suggest strong winds can lead to dispersal velocities several times greater than expected under prevailing conditions.

Rafting can be a key dispersal mechanism for many marine species that lack autonomous transoceanic dispersal abilities (Nikula et al. 2010, Cumming et al. 2014). Live epibiota were detected on many of the beach-cast rafts sampled in the present study, including several low-dispersal molluscan taxa that exhibit strong genetic connectivity among disjunct coastal populations (Nikula et al. 2013). Interestingly, the detection of live epibiota (e.g. chitons and coralline algae) on some holdfast clasts themselves (Fig. 4c) suggests that rafting rock, in addition to floating biological substrates, may help to enhance biological dispersal.

CONCLUSIONS

Broadly, the present study highlights that storms can greatly increase the speed of marine rafting, potentially leading to dispersal timeframes that are several times (e.g. 3- to 5-fold) faster than would be predicted under standard oceanographic circulation models. These data thus have important implications for our understanding of rafting dispersal potential between otherwise isolated coastal regions and populations.

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LITERATURE CITED

- ✦ Ali JR, Huber M (2010) Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature* 463:653–656
- ✦ Briggs JC (1974) *Marine biogeography*. McGraw-Hill, New York, NY
- ✦ Bussolini LT, Waters JM (2015) Genetic analyses of rafted macroalgae reveal regional oceanographic connectivity patterns. *J Biogeogr* 42:1319–1326
- ✦ Carlton JT, Chapman JW, Geller JB, Miller JA and others (2017) Tsunami-driven rafting: transoceanic species dispersal and implications for marine biogeography. *Science* 357:1402–1406
- ✦ Carter RM, Lindqvist J (1975) Sealers Bay submarine fan complex, Oligocene, southern New Zealand. *Sedimentology* 22:465–483
- ✦ Censky EJ, Hodge K, Dudley J (1998) Over-water dispersal of lizards due to hurricanes. *Nature* 395:556
- ✦ Chiswell SM (1996) Variability in the Southland Current, New Zealand. *NZ J Mar Freshw Res* 30:1–17
- ✦ Chiswell SM, Wilkin J, Booth JD, Stanton B (2003) Trans-

- Tasman Sea larval transport: Is Australia a source for New Zealand rock lobsters? *Mar Ecol Prog Ser* 247: 173–182
- ✦ Collins CJ, Fraser CI, Ashcroft A, Waters JM (2010) Asymmetric dispersal of southern bull kelp (*Durvillaea antarctica*) adults in southern New Zealand: testing an oceanographic hypothesis. *Mol Ecol* 19:4572–4580
- ✦ Craw D, Waters JM (2018) Long distance kelp-rafting of rocks around southern New Zealand. *NZ J Geol Geophys*, doi:10.1080/00288306.2018.1492424
- ✦ Cumming RA, Nikula R, Spencer HG, Waters JM (2014) Transoceanic genetic similarities of kelp-associated sea slug populations: Long-distance dispersal via rafting? *J Biogeogr* 41:2357–2370
- ✦ Fraser CI, Nikula R, Waters JM (2011) Oceanic rafting by a coastal community. *Proc R Soc B* 278:649–655
- ✦ Fraser CI, Kay GM, Plessis MD, Ryan PG (2017) Breaking down the barrier: dispersal across the Antarctic Polar Front. *Ecography* 40:235–237
- Fraser CI, Morrison AK, Hogg AM, Macaya EC and others (2018) Antarctica's ecological isolation will be broken by storm-driven dispersal and warming. *Nat Clim Change* 8:704–708
- ✦ Garden CJ, Craw D, Waters JM, Smith A (2011) Rafting rocks reveal marine biological dispersal: a case study using clasts from beach-cast macroalgal holdfasts. *Estuar Coast Shelf Sci* 95:388–394
- ✦ Garden CJ, Currie K, Fraser CI, Waters JM (2014) Rafting dispersal constrained by an oceanographic boundary. *Mar Ecol Prog Ser* 501:297–302
- ✦ Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by flow. *Am Nat* 155:769–789
- ✦ Gillespie RG, Baldwin BG, Waters JM, Fraser CI, Nikula R, Roderick GK (2012) Long-distance dispersal: a framework for hypothesis testing. *Trends Ecol Evol* 27:47–56
- ✦ Harrold C, Lisin S (1989) Radio-tracking rafts of giant kelp: local production and regional transport. *J Exp Mar Biol Ecol* 130:237–251
- ✦ Hawes NA, Taylor DI, Schiel DR (2017) Transport of drifting fucoid algae: nearshore transport and potential for long distance dispersal. *J Exp Mar Biol Ecol* 490:34–41
- ✦ Hernandez-Carmona G, Hughes B, Graham MH (2006) Reproductive longevity of drifting kelp *Macrocystis pyrifera* (Phaeophyceae) in Monterey Bay, USA. *J Phycol* 42:1199–1207
- ✦ Hobday AJ (2000) Abundance and dispersal of drifting kelp *Macrocystis pyrifera* rafts in the Southern California Bight. *Mar Ecol Prog Ser* 195:101–116
- ✦ Krauss W, Dengg J, Hinrichsen HH (1989) The response of drifting buoys to currents and wind. *J Geophys Res* 94: 3201–3210
- ✦ Monzón-Argüello C, Dell'Amico F, Morinière P, Marco A and others (2012) Lost at sea: genetic, oceanographic and meteorological evidence for storm-forced dispersal. *J R Soc Interface* 9:1725–1732
- ✦ Nikula R, Fraser CI, Spencer HG, Waters JM (2010) Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. *Mar Ecol Prog Ser* 405:221–230
- ✦ Nikula R, Spencer HG, Waters JM (2013) Passive rafting is a powerful driver of transoceanic gene flow. *Biol Lett* 9: 20120821
- ✦ Poulain PM, Gerin R, Mauri E, Pennel R (2009) Wind effects on drogued and undrogued drifters in the eastern Mediterranean. *J Atmos Ocean Technol* 26:1144–1156
- ✦ Rio MH (2012) Use of altimeter and wind data to detect the anomalous loss of SVP-type drifter's drogue. *J Atmos Ocean Technol* 29:1663–1674
- Skerman TM (1958) Rates of growth in two species of *Lepas* (Cirripedia). *NZ J Sci* 1:402–411
- ✦ Smith SDA (2002) Kelp rafts in the Southern Ocean. *Glob Ecol Biogeogr* 11:67–69
- ✦ Strong DT, Turnbull RE, Haubrock S, Mortimer N (2016) Petlab: New Zealand's national rock catalogue and geo-analytical database. *NZ J Geol Geophys* 59:475–481
- Thiel M, Gutow L (2005) The ecology of rafting in the marine environment. I. The floating substrata. *Oceanogr Mar Biol Annu Rev* 42:181–264
- Thiel M, Haye PA (2006) The ecology of rafting in the marine environment. III. Biogeographical and evolutionary consequences. *Oceanogr Mar Biol Annu Rev* 44:323–429
- Turnbull IM, Allibone AH, Jongens R (2010) Geology of the Fjordland area: scale 1:250 000. Institute of Geological and Nuclear Sciences, Lower Hutt
- ✦ Waters JM, Craw D (2017) Large kelp-rafted rocks as potential dropstones in the Southern Ocean. *Mar Geol* 391: 13–19
- ✦ Waters JM, King TA, Fraser CI, Craw D (2018) Crossing the front: contrasting storm-forced dispersal dynamics revealed by biological, geological and genetic analysis of beach-cast kelp. *J R Soc Interface* 15:20180046
- ✦ White C, Selkoe KA, Watson J, Siegel DA, Zacherl DC, Toonen RJ (2010) Ocean currents help explain population genetic structure. *Proc R Soc B* 277:1685–1694

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