NOTE

Rafting dispersal constrained by an oceanographic boundary

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ABSTRACT: The role of oceanographic processes in mediating passive marine dispersal events is poorly understood. We conducted transect surveys across the subtropical front (STF), a major oceanographic boundary, to test the hypothesis that this physical feature constrains the rafting of detached macroalgae. Specifically, we used genetic analysis to assess the geographic origins of floating bull-kelp *Durvillaea antarctica* specimens in southern New Zealand. Nearly half of the floating specimens sampled immediately beyond the STF (30 to 60 km offshore) were shown to have distant subantarctic origins, despite their proximity to the New Zealand mainland at the time of sampling. These results suggest that the biogeographic composition of rafting communities is often predictable based on oceanographic features, but also imply that strong wind events have the potential to modify such patterns.

KEY WORDS: Biogeography · Biological oceanography · Connectivity · *Durvillaea antarctica* · Kelp · Raft

INTRODUCTION

Understanding the links between marine biological and physical oceanographic processes is a key goal in ocean science (Lalli & Parsons 1997, Largier 2003). Biologists have long recognised that marine biodiversity patterns are often correlated with the distributions of distinct water masses (Mackas et al. 1985, Gaylord & Gaines 2000, Gilg & Hilbish 2003, Zakas et al. 2009). However, our understanding of the biological effects of oceanographic features, particularly in the context of passive rafting events (Reusch 2002, Thiel & Haye 2006), remains very limited.

Detached, buoyant macroalgae are a prominent feature of temperate and high-latitude oceans, particularly in the Southern Hemisphere (e.g. *Durvillaea*

antarctica and *Macrocystis pyrifera*; Smith 2002, Thiel & Gutow 2005). Such rafts likely play an important role in facilitating dispersal and connectivity between coastal marine floral and faunal communities (Ingólfsson 1995, Hobday 2000a, Thiel & Haye 2006, Nikula et al. 2010). However, owing to the logistical difficulties of tracking individual rafts, there is a lack of information on the role of oceanographic processes in mediating this passive dispersal in the marine environment (but see Collins et al. 2010, Macreadie et al. 2011).

The waters off eastern New Zealand (NZ) are strongly influenced by the subtropical front (STF, sometimes termed the subtropical convergence, STC), a major circumglobal oceanographic boundary zone between warm (subtropical) and cool (subantarctic) water masses (Fig. 1). Transects across the STF in the
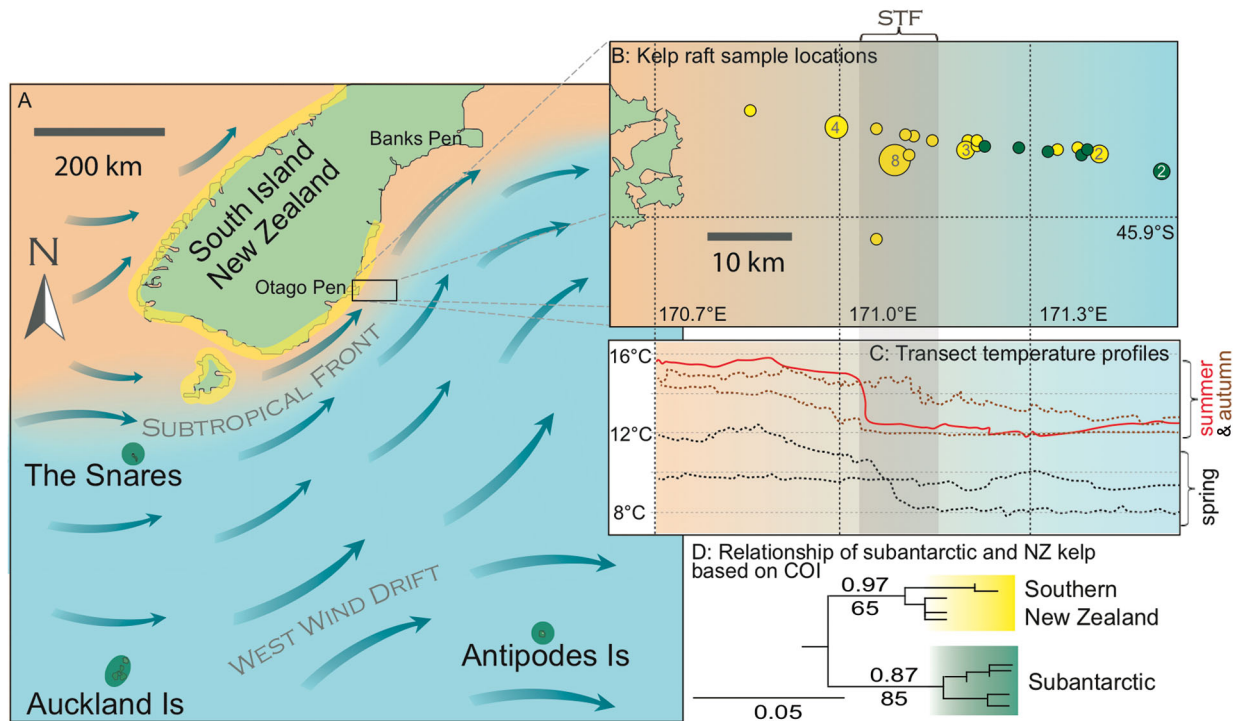
Fig. 1. *Durvillaea antarctica.* Genetic assessment of bull-kelp rafts drifting up to 60 km east of New Zealand. (A) Regional oceanographic features including surface currents (blue arrows, simplified after Chiswell 2009) and the subtropical front (STF; thermal gradient from temperate [orange] to cool [blue] water). The distributions of 2 genetic lineages of bull-kelp are indicated by green (subantarctic clade) and yellow (southern New Zealand clade) lines. (B) Locations of rafts sampled during 6 transects, with clade indicated by color (yellow or green). Where multiple rafts were collected from the same location, sample size is indicated by circle size. (C) Thermal profile of surface water along 5 of the transects (2 in spring, 1 in summer, 2 in autumn). (D) Phylogenetic tree based on mtDNA showing divergence between the 2 kelp clades, from Bayesian and maximum-likelihood analyses performed by Fraser et al. (2011). Numbers above nodes are posterior probability values from Bayesian analysis, and numbers below nodes indicate bootstrap support from maximum likelihood analysis (1000 replicates)

NZ region have previously revealed marked discontinuities in epipelagic zooplankton communities (Jillett 1976) and in mesopelagic fish, crustacean and cephalopod distributions (Robertson et al. 1978). Additionally, several recent genetic studies of coastal marine species in the NZ region have revealed substantial genetic disjunctions across this oceanographic transition zone (Boessenkool et al. 2009, Fraser et al. 2011). These findings suggest that the STF may represent an important barrier to biological dispersal in this region. In particular, we predict that the STF may limit rafting dispersal, and thus influence connectivity patterns among coastal communities.

The STF lies approximately 30 km east of Otago (southeast NZ), and the surface water immediately beyond this front is of subantarctic origin (Fig. 1). Subantarctic bull-kelp *Durvillaea antarctica* has been found washed up on south-eastern NZ beaches following easterly storms (Collins et al. 2010, Fraser et al. 2011), but these rafts are relatively few in number compared to rafts of local origin. If the STF does

indeed act as a barrier to dispersal for macroalgal rafts, there may nonetheless be substantial quantities of subantarctic-origin specimens floating close and parallel to the NZ mainland coast, which are generally unable to cross the STF and achieve landfall in NZ. We hypothesised that *D. antarctica* specimens floating near to shore, west of the STF, would be predominantly of NZ mainland origin, whereas specimens to the east of the STF would have come from more distant, subantarctic sources.

We conducted biological transect surveys across the STF and used genetics to assess the regional origins of kelp rafts. Our results give important insights into the biological significance of this oceanographic barrier. While previous studies have analysed the origins of beach-cast kelp rafts to test oceanographic hypotheses (Collins et al. 2010), or have assessed the distributions of floating macroalgae (Hobday 2000a,b, Hinojosa et al. 2010, 2011), to our knowledge, this is the first study to use genetic analysis to assess the distribution and origins of kelp rafts at sea.

MATERIALS AND METHODS

We collected 36 floating specimens of southern bull-kelp at sea along a 60 km easterly-trending transect off the Otago coast on 6 trips during 2011 and 2012 (Fig. 1), aboard the University of Otago research vessel RV 'Polaris II'. Transect dates were: 10 January, 1 and 23 March, 23 September and 8 November 2011; and 10 January 2012. This transect encompasses both inshore (modified subtropical and neritic) and offshore (subantarctic) water types, separated by the STF around 30 to 40 km offshore (Currie et al. 2011). Continuous sea surface temperature and salinity profiles were measured along the transect using a Seabird thermosalinograph (Model SBE 21). The transition from subtropical to subantarctic water is characterised at the surface by a rapid reduction in SST and salinity, and the STF is typically constrained by the 500 m isobaths. The subantarctic surface water (SASW) is defined as water at approximately the 10°C isotherm in winter and the 12°C isotherm in summer (Gonsior et al. 2011, Jones et al. 2013).

Attempts were made to collect all floating kelp specimens observed at sea. Specifically, specimens were retrieved from the sea using grappling hooks, and locations were recorded using a GPS. Specimens were stored frozen in plastic bags prior to genetic analysis. Genomic DNA was extracted from each specimen using Chelex 100 (Walsh et al. 1991), and a 629 bp fragment of mitochondrial cytochrome *c* oxidase subunit I (COI) DNA was sequenced for each specimen using primers GazF1 and GazR1 (Saunders 2005), following the protocol of Fraser et al. (2009a). Base calls were made by eye using Sequencher 4.9 (Gene Codes), with no insertions or deletions detected, and sequences were aligned by eye. Phylogenetic relationships among sequences (including allocation of haplotypes to subantarctic versus NZ mainland clades), and haplotype identity with respect to published reference haplotypes (Fraser et al. 2009a,b, 2011, Collins et al. 2010) were determined using PAUP*4.0b10 (Swofford 2002).

RESULTS

Temperature profiles across the majority of transects confirm that the STF generally lies at a longitude around 171.10 to 171.15° E (Fig. 1; approximately 28 to 30 km offshore), with the cold SASW lying directly east of this front (>171.15° E; >30 km offshore), and a warmer coastal water mass directly to the west (<171.10° E; <28 km offshore).

Partial COI sequences of rafting kelp specimens revealed a total of 7 distinct haplotypes (Table 1), with the vast majority of specimens (34 of 36) yielding sequences identical to published reference haplotypes from attached *Durvillaea antarctica* populations (Fraser et al. 2009b, 2011). Phylogenetic analysis facilitated clear discrimination between 'mainland-origin' versus 'subantarctic-origin' kelp haplotypes (i.e. phylogenetic placement within the 'NZ South' versus 'subantarctic' clades; Fig. 1). Of the specimens collected from coastal waters at the western end of the transect (<171.15° E, <30 km offshore, within or west of the STF), all 19 (100%) originated from the mainland NZ clade, with no (0%) subantarctic haplotypes detected in this inshore region. By contrast, of the 17 specimens sampled from cool subantarctic waters at the eastern end of the transect (171.15–171.5° E, 30 to 60 km offshore; east of the STF), 10 (59%) were determined as having mainland origins, and 7 (41%) as having subantarctic origins. Based on published genetic data (Fraser et al. 2009b, 2011), 6 of these 7 subantarctic specimens (all exhibiting the same haplotype, 'Subant-2', referred to as 'T-16' by Fraser et al. 2011) likely originated from the Snares and/or Auckland Islands, some 450 and/or 650 km SSW of their ultimate collection localities, respectively. Sample B4 (new haplotype 'Subant-9') differs from Subant-2 by a single substitution and belongs to the same Auckland/Snares haplogroup, so it likely originated from the same subantarctic region. All of these subantarctic-origin specimens were characterised by dense coverings of epifaunal barnacles (*Lepas australis*), consistent with previous observations (Fraser et al. 2011).

Notably, of the 10 'NZ mainland' specimens detected at the eastern end of the transect (more than 30 km offshore), the majority (7) were collected on a single trip (8 November 2011) that was undertaken in the immediate aftermath of a 3 d period of continuous northwesterly winds (4–7 November 2011). This weather system contrasts with the prevailing southwesterly and northeasterly winds that generally characterise the region (Fraser et al. 2011). This November northwesterly system may have transported these specimens east across the STF. With the exception of this November 2011 transect, there is a near-perfect concordance between kelp origin (mainland versus subantarctic) and transect location (east versus west).

DISCUSSION

Our results indicate an association between spatial structuring of oceanographic and biological features.

Table 1. *Durvillaea antarctica*. Geographic and genetic details of detached specimens sampled for genetic analysis. 'Distance' refers to distance from shore

Date Sample	Latitude (°S)	Longitude (°E)	Distance (km)	Haplotype	GenBank accession
10 Jan 2011					
A06	45.8239	171.0839	26	NZSth-1	FJ550089
A07	45.8239	171.0839	26	NZSth-1	FJ550089
A08	45.8239	171.0839	26	NZSth-1	FJ550089
A10	45.8239	171.0839	26	NZSth-1	FJ550089
A11	45.8239	171.0839	26	NZSth-1	FJ550089
A12	45.8239	171.0839	26	NZSth-9[a]	KJ144654
A13	45.8239	171.0839	26	NZSth-1	FJ550089
A14	45.8239	171.0839	26	NZSth-1	FJ550089
A15	45.8238	171.1013	28	NZSth-1	FJ550089
A16	45.9123	171.0532	25	NZSth-1	FJ550089
1 Mar 2011					
B3	45.8076	171.1947	35	NZSth-2	FJ550106
B4	45.8340	171.4995	59	SubAnt-9[a]	KJ144655
B5	45.8340	171.4995	59	SubAnt-2	FJ550102
23 Mar 2011					
C1	45.7918	170.9951	19	NZSth-1	FJ550089
C2	45.7918	170.9951	19	NZSth-1	FJ550089
C3	45.7918	170.9951	19	NZSth-1	FJ550089
C5	45.7918	170.9951	19	NZSth-1	FJ550089
C6	45.8129	171.2180	37	SubAnt-2	FJ550102
C7	45.8147	171.2710	41	SubAnt-2	FJ550102
C8	45.8189	171.3175	45	SubAnt-2	FJ550102
C9	45.8220	171.3696	48	SubAnt-2	FJ550102
23 Sep 2011					
D1	45.7777	170.8546	9	NZSth-6	FJ550108
D3	45.8018	171.0948	27	NZSth-1	FJ550089
D4	45.8024	171.1079	28	NZSth-1	FJ550089
D7	45.8134	171.2033	36	NZSth-1	FJ550089
D8	45.8187	171.3315	46	NZSth-1	FJ550089
8 Nov 2011					
E01	45.8069	171.1379	30	NZSth-2	FJ550106
E02	45.8141	171.1950	35	NZSth-7	HQ166840
E03	45.8137	171.2086	36	NZSth-1	FJ550089
E04	45.8137	171.2086	36	NZSth-7	HQ166840
E05	45.8137	171.2086	36	NZSth-2	FJ550106
E10	45.8148	171.3635	48	NZSth-2	FJ550106
E11	45.8172	171.3810	49	SubAnt-2	FJ550102
E12	45.8190	171.3971	50	NZSth-1	FJ550089
E13	45.8190	171.3971	50	NZSth-1	FJ550089
10 Jan 2012					
F2	45.7954	171.0527	24	NZSth-1	FJ550089
[a]COI haplotypes new to this study					

Specifically, the location of the STF relative to kelp raft collection location can often be a predictor of the origin of rafting assemblages, with bull-kelp specimens located offshore (east of the front) versus inshore often arising from distinct subantarctic versus mainland source regions, respectively. The genetically distinct rafting assemblages broadly delineated by the STF reinforce previous observations of distinct epipelagic and mesopelagic faunal communities apparently defined by this front (Jillett 1976, Robertson et al. 1978). Overall, our results support the hypothesis that oceanographic connectivity can play a substantial role in shaping marine biodiversity patterns (Gaylord & Gaines 2000). Additionally, we suggest that passively dispersing planktonic and buoyant rafting taxa may be similarly influenced by ocean currents (White et al. 2010).

At the outset of the study, we predicted that the STF represents a barrier for macroalgal rafting events. Although these results indicate that the geographic origins of the rafts are indeed predictable based on their location relative to the STF, at least in 5 of 6 transect surveys undertaken here, they also suggest that strong weather systems (e.g. as occurred in early November 2011) have the potential to locally distort such patterns by transporting substantial numbers of specimens across this oceanographic boundary. This finding mirrors the previous observations of subantarctic kelp specimens crossing the STF to reach the New Zealand shore after extended easterly weather systems (Fraser et al. 2011).

Nevertheless, our data highlight the fact that oceanographic connectivity, rather than geographic proximity per se, can be an important predictor of biogeographical relationships (Burridge et al. 2006). Specifically, rafting assemblages within 30 to 60 km of the NZ mainland arguably have a closer biological relationship to those of the subantarctic islands — some 600 km south or farther — than they do to those a few kilometres farther inshore.

It is well established that wind conditions can substantially affect oceanographic conditions (Price 1981) and also directly influence rafting trajectories (Harrold & Lisin 1989, Tapia et al. 2004, Hernandez-Carmona et al. 2006, Rothäusler et al. 2012). In particular, there is mounting evidence that storms can play an important role in mediating long-distance oceanic rafting journeys (Censky et al. 1998, Fraser et al. 2011, Gillespie et al. 2012). Additionally, a recent multidisciplinary review concluded that storm-forced dispersal likely plays a

substantial role in shaping connectivity of pelagic taxa (Monzón-Argüello et al. 2012). Future studies should extend the approach outlined here to further assess the combined roles of strong weather systems and oceanographic features in shaping dispersal in the marine environment.

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