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Transport of drifting fucoid algae: Nearshore transport and potential for long distance dispersal

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ABSTRACT

Processes responsible for transporting detached macroalgae through the nearshore environment and offshore to where long distance dispersal (LDD) can occur have rarely been examined. Here, we test the influence of nearshore winds, tidal currents and position of release (low, mid or high tidal zone) on the dispersal of drifting fucoid algae were tested. "Drift sets" (tagged Hormosira banksii, Durvillaea antarctica, Cystophora torulosa and GPS drifters) were tracked over single tidal cycles. Wind direction had the greatest effect on movement of drift sets, but interacted with tidal direction. Overall, offshore winds and outgoing tides were most favourable for LDD, but their effect differed between species. Approximately 90% of H. banksii, *D. antarctica* and GPS-tracked drifters were beach-cast after one tidal cycle during onshore winds, while 19% were beach-cast during offshore winds. In contrast, 50–75% of *C. torulosa* were beach-cast after one tide, regardless of wind direction. Displacement of drifters was affected by tidal zone of release, but interacted with wind and tidal direction. Drifting velocities varied between drifter types, with surface drifters travelling further and faster than the benthic-drifting species. Analysis of 20 years of wind data found seasonal differences in the percentage of hourly winds, with greater periods of south-westerly and north-westerly winds, and fewer onshore north-easterly winds, during autumn and winter periods. Conditions for successful offshore dispersal from the major algal dominated peninsulas of southern New Zealand are, therefore, more likely to occur if detachment of algae occurs during outgoing tides in autumn and winter.

1. Introduction

Long distance dispersal (LDD) is fundamental to population connectivity, range expansion and gene flow, and is crucial for understanding the potential impacts of invasive species (Kinlan and Gaines, 2003, Schiel, 2004, Schiel and Foster, 2006, Thiel and Haye, 2006). In shallow-coast marine environments, dispersal involves complex interactions between physical conditions, such as wind, tides and currents, and the properties of the dispersing species, particularly their buoyancy (Norton, 1992, Gaylord et al., 2002, 2004, 2006, Stevens et al., 2008, Taylor et al., 2010). For habitat-dominating marine algae, it is thought that most LDD occurs via drifting adults or fertile plant fragments that have become detached from the substratum and are subsequently transported by prevailing currents (van den Hoek, 1987, Kinlan and Gaines, 2003), although the relative contribution of dispersing propagules such as spores and zygotes is only beginning to be understood (Reed et al., 2000, Gaylord et al., 2004, 2006, Taylor et al., 2010).

Algae that detach from the substratum can travel considerable distances due to tidal and wind-induced movement of surface waters, if they do not immediately wash ashore (Thiel and Gutow, 2005, Lapointe et al., 2014). Before drifting algae can become entrained in large-scale offshore current systems, however, they must first move through the turbulent nearshore environment and away from coastal reefs. This nearshore environment is hydrodynamically complex, and the short-term movement of drift may be strongly influenced by wind and tidal currents, bathymetry, and waves (Ochieng and Erftemeijer, 1999). The conditions favourable for movement of drifting algae offshore, and the frequency of offshore dispersal events, are not known for most species.

Several studies have tracked the movement of naturally occurring or artificially created drifters (Harrold and Lisin, 1989, Hobday, 2000, Hernandez-Carmona et al., 2006, Muhlin et al., 2008), but few of these drifters originated from the shoreline. For example, Harrold & Lisin (1989)) found that rafts of giant kelp, *Macrocystis pyrifera* (L.) C.A. Agardh, released 0.2 to 4.6 km away from the coast within Monterey Bay, California were transported according to prevailing winds, which determined the movement of the surface waters. In the Southern California Bight, the trajectories of satellite-tracked drifters, deployed at an average distance of 12.3 km from the nearest land, followed

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large-scale circulation patterns, which were stronger than the wind-influenced surface flow (Hobday, 2000). Hobday (2000) defined a 'successful connection event' between populations to be drifters that were deployed <10 km from the coast, and ended up <5 km from the coast. Under this definition, 45% of drifters were successful in connecting populations but because no drifters were released from the shoreline, these data are only representative of drift material that had already moved some distance offshore (Hobday, 2000). Closer to shore, Muhlin et al. (2008) used 1700 drifters, in the form of labelled oranges, and tagged algae to determine the influence of circulation patterns on the genetic structure of *Fucus vesiculosus* L. They used 17 deployments, from the high tide mark to 100 m offshore, and two GPS drifters to track local circulation patterns. They concluded that genetic structure was best explained by rafting of storm-detached adults that drift and release gametes at new sites. They also found there could be multiple dispersal trajectories from a single site on different days, depending on sea conditions.

Dispersal by marine algae can therefore be a complex process influenced by a variety of physical and biological factors, including the characteristics of adult plants and interactions with the nearshore water mass (Lapointe et al., 2014). The initial export phase of drifting algae from the intertidal zone must be linked to particular nearshore conditions and species characteristics. Despite this, the ability of detached algae to move offshore and then back again for release of gametes onto rocky shores remains poorly understood. The extent of dispersal may depend on the release points of algae, and certain times of the year may be more favourable for retention or for dispersal offshore (McKenzie and Bellgrove, 2008). Furthermore, the relative ability of drifting algae to move offshore after detachment may vary between species. Drifting algae can be exported to nearby or distant sites either as benthic drift suspended near the sea floor (Harrold and Reed, 1985, Holmquist, 1994, Belsher and Meinesz, 1995, Brooks and Bell, 2001) or as floating algae in the surface waters, and the location of drift within the water column (related to buoyancy) may influence their dispersal potential (Waters, 2008). Because of vertical shear in the water column (Stevens et al., 2008), algae drifting near the seabed may be entrained in currents moving at different velocities and in different directions than those within the surface waters. Furthermore, to connect populations effectively drift algae must be reproductively viable, and dispersal potential will therefore depend on the reproductive periodicity of the species.

In southern New Zealand, the fucoid algae *Hormosira banksii* (Turner) Decaisne, *Durvillaea antarctica* (Chamisso) Hariot and *Cystophora torulosa* (R. Brown) J. Agardh dominate the intertidal zones of most rocky shore platforms along thousands of km of coastline (Schiel, 2006, 2011), and contribute a significant portion of the coastal drift and beach-cast seaweed (Hawes, 2008). The bull kelp *D. antarctica* has been reported to be the dominant floating algal species in the Southern Ocean (Smith, 2002) and is frequently cast ashore in regions where it does not grow (e.g., the Kermadec islands, 800 km north of mainland New Zealand; Adams, 1994). Similarly, drifting *H. banksii* has been recorded to be transported by currents and cast ashore at distant sites (Adams, 1994, McKenzie and Bellgrove, 2008). This species is common on the middle to lower shore and consists of air- and fluid-filled vesicles, which float on the sea surface when detached. It is a dioecious species that is reproductive throughout the year (Osborn, 1948), but has large pulses of reproduction during the warmer months (September–January) (Taylor and Schiel, 2003). *D. antarctica* is a dioecious species that is reproductive from May to August (late autumn through winter) (Clayton, 1990, Taylor and Schiel, 2005). It is found at low water on exposed and moderately wave-exposed reefs and is buoyant due to an internal honeycomb structure of fronds. In contrast to *H. banksii* and *D. antarctica, C. torulosa* dominates the low intertidal and immediate subtidal zones on semi-sheltered reefs and is not as buoyant as the other species. Detached plants tend to drift low in the water column and often near the sea floor. *C. torulosa* is monoecious, producing one egg per oogonium and is reproductive from late spring through summer (Schiel, 2006).

These interspecific differences could have important ecological and evolutionary consequences for these species which may be reflected in their distributions. For example, *Cystophora torulosa* is confined to New Zealand and a small area of southern Australia (Tasmania and Victoria) (Womersley, 1959, 1964). In contrast, *Hormosira banksii*, is also found in New Zealand and southern Australia, but has a more extensive distribution which includes Norfolk and Lord Howe Islands (Adams, 1994). Of the fucoid algae examined here, *Durvillaea antarctica* has the widest distribution, spanning the Subantarctic Islands and the southern South American coasts of Chile and Argentina (Adams, 1994, Fraser et al., 2009, Collins et al., 2010, Bussolini and Waters, 2015). Furthermore, the trans-oceanic distributions of invertebrate species have been attributed to rafting in *Durvillaea antartica* holdfasts (Donald et al., 2005), while non-buoyant *Durvillaea* species are geographically restricted (Waters, 2008).

An understanding of their potential for short and long range dispersal is fundamental to local population dynamics, and is an essential component of general models of community structure (Schiel, 2004). Despite this, very little is known about the potential importance of drifting as a long-distance dispersal mechanism for these key species that are known drivers of diversity along much of the southern shores of New Zealand and southeastern Australia (Bellgrove et al., 2004, Schiel, 2004, Schiel and Foster, 2006, Schiel, 2011). This paper specifically test the influence of nearshore processes on the initial phase of dispersal, the period immediately after the detachment of an adult plant from an intertidal shore, with particular reference to the relative importance of wind (onshore/offshore) versus tidal currents (incoming/outgoing), and whether their influences vary between species. The average drifting velocities and overall linear displacement of drifters were determined as well as whether detachment location within the tidal zone (low, mid or high shore) influences the movement of drift.

2. Materials and methods

Algal drift experiments were done on ten occasions in March and April 2008 (New Zealand Autumn) (Table 1) in the nearshore waters of a coastal embayment in Kaikoura (42° 25″ 14″ S, 173° 41″ 41″ E), located on the east coast of the South Island of New Zealand (see supplement 1). Oceanic circulation patterns around Kaikoura are complex and are influenced by the interaction of nearshore water masses with the coastal bathymetry, wind-driven currents, and tides (Chiswell and Schiel, 2001). Tide tables for the area were obtained from Land Information New Zealand (LINZ), and wind speed and direction data were obtained from the Kaikoura Automatic Weather Station (42° 25″ 15″ S, 173° 41″ 27″ E), courtesy of the National Institute of Water and Atmospheric Research, New Zealand, CLIFLO database (cliflo.niwa.co.nz).

Table 1
Deployment dates, tide and wind direction, wind speed range and estimated maximum wave heights during drifter experiments.

Experiment	Deployment date	Tide direction	Wind direction	Wind speed range ($m s^{-1}$)	Maximum wave height estimate (m)
1	19.3.08	Incoming	Onshore	2.6–5.1	0.5
2	21.3.08	Incoming	Onshore	2.1–2.5	0.25
3	22.3.08	Outgoing	Offshore	5.1–10.3	1
4	22.3.08	Incoming	Offshore	5.7–8.2	1
5	3.4.08	Incoming	Onshore	2.6–8.8	1
6	4.4.08	Incoming	Onshore	2.1–3.1	0.25
7	16.4.08	Incoming	Offshore	3.6–5.1	0.5
8	16.4.08	Outgoing	Onshore	2.1–3.1	0.25
9	17.4.08	Outgoing	Onshore	1.5–3.1	0.25
10	18.4.08	Outgoing	Offshore	2.1–17.5	1.5