Nearshore Dispersal and Reproductive Viability of Intertidal Fucoid Algae: how effective is drift in local to regional dispersal?

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Abstract

The ecological importance of drifting will depend on the abundance of drifting algae and whether it is reproductively viable. However, the ability of adult plants to successfully disperse long-distances by drifting is largely unknown, particularly for fucoids. The abundance, species composition, and reproductive status of drifting algae was examined by transect surveys around Kaikoura and Banks Peninsula. Abundance and species composition varied between sites, but all drifting algae that were in reproductive season, and had reproductive structures intact, were reproductively active.

The reproductive longevity and viability of drifting and beach-cast *Hormosira banksii*, *Durvillaea antarctica* and *Cytophora torulosa* was compared with attached populations. Drifting algae remained reproductively viable, and fecundity did not differ from that of attached algae. Viable propagules were released from drifting algae for the duration of the experiments (*H. banksii* 57 days, *D. antarctica* 62 days, and *C. torulosa* 43 days). In contrast, beach-cast algae ceased to release propagules after 14 days.

Dispersal by drifting relies on offshore transport after detachment. To determine the influence of wind and tidal currents on the nearshore transport of drifting algae, tagged *H. banksii*, *D. antarctica*, *C. torulosa* and GPS-tracked drifters were released from shore. Drifters generally moved in the direction of the prevailing wind, but some influence of tidal direction and bathymetry was detected. Offshore winds and outgoing tides were favourable for the offshore transport of surface drifting algae.

Following dispersal and arrival at new locations, the distance between gametes may be important in determining the fertilisation success of dioecious species. Experiments testing the fertilisation success of *H. banksii* and *D. antarctica*, over increasing distances, showed that fertilisation success decreased with increasing distance between male and female gametes. Despite this, eggs were fertilised when male and female gametes were up to 2m apart, and sperm remained viable for 2 hours.

Chapter 1 - General Introduction

The role of dispersal in structuring communities

Dispersal is a fundamental process in population dynamics (Gadgil 1971, Nathan and Muller-Landau 2000). The scale and patterns of dispersal can determine the scale at which species interact with each other and their environment, how they respond to disturbance, and evolve (Sousa 2001, Kinlan and Gaines 2003). Information on dispersal is essential for understanding spatial and temporal patterns of distribution, range expansion, invasions, and the genetic structure of populations, and is crucial for marine reserve design, and understanding the potential impacts of invasive species (Kinlan and Gaines 2003, Shanks *et al.* 2003, Schiel 2004, Schiel and Foster 2006).

Dispersal ability is largely a product of the characteristics of early life stages, especially propagules, and reproductive adults, interacting with the nearshore environment (Schiel 2004, Schiel and Foster 2006). The arrival of dispersive propogules, or drifting adult plants, then influences settlement, and subsequent recruitment (Menge and Branch 2001). These factors interact, and are variable over several temporal and spatial scales (Hruby and Norton 1979, Caffey 1985, Connell 1985, Hoffmann 1987, Raimondi 1990, Santelices 1990) and, consequently, the degree of connectivity between populations can be quite different (Schiel 2004). However, despite the importance of dispersal to marine community structure, highlighted in recent reviews on dispersal of marine organisms (Kinlan and Gaines 2003, Shanks *et al.* 2003), information on the dispersal of marine algae is generally sparse (Kinlan and Gaines 2003, Schiel 2004, Schiel and Foster 2006).

Dispersal by marine algae

Large brown algae (fucoids and laminarians) are dominant components of rocky reef communities worldwide. They add three-dimensional structure to rocky reefs and form canopies that provide shelter, food, and habitat for many other species (Jones *et al.* 1994, Schiel *et al.* 1995, Schiel 2004, 2006, Schiel and Foster 2006). Given the importance of marine algae to rocky shore communities, knowledge of their dispersal is fundamental for understanding local population dynamics and is an essential component of general models of community structure (Schiel 2004).

Dispersal estimates for algae are very broad, ranging from only a few meters to tens of kilometres, and depend on the mode of dispersal and species characteristics (Fig. 1.1). Marine invertebrates can potentially disperse relatively long distances because they have an obligate planktonic period, and are motile. In contrast, most marine algae do not have an obligate planktonic stage, and have non-motile, negatively buoyant gametes, or spores with limited motility. Organisms with no planktonic larval stage have relatively short dispersal estimates, typically less than 1km (Kinlan and Gaines 2003). However, if they have a secondary mechanism of dispersal, such as drifting reproductive adults, dispersal distances may be much longer.

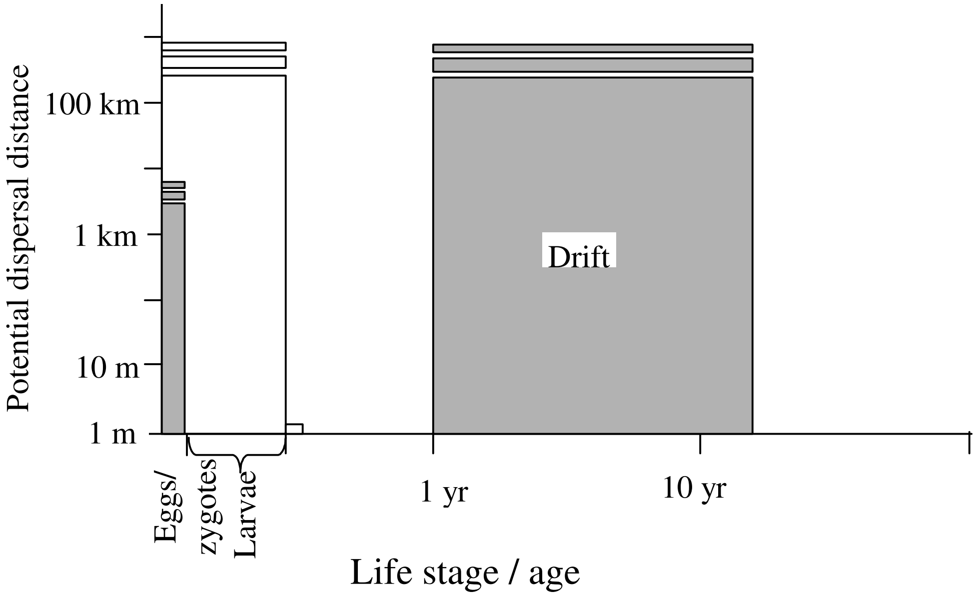


Figure 1.1: Diagram comparing potential dispersal distance of laminarian and fucoid algae (shaded bars) with sessile invertebrates (open bar) at different stages of development.''Drift'' represents detached, floating, reproductive plants. From Schiel (2004).

Many marine algae are potentially capable of dispersing both as propagules and as drifting adults (Schiel 2004, Schiel and Foster 2006). Large brown algae dominate the drifting macroalgae observed throughout the world (reviewed in Thiel and Gutow 2005a). Many species are positively buoyant as adults, due to air-filled bladders and fronds. This allows entire plants and plant fragments to float to the sea surface following detachment from the substratum, and potentially to drift to distant sites. Organisms that have no planktonic larvae stage, but that do have a secondary mechanism of dispersal such as drifting, have dispersal estimates of 10km or more (Kinlan and Gaines 2003). Such distances suggest that drifting algae could play an important role in population connectivity. However, the relative ability of marine algae to disperse as propagules, or via drifting reproductively viable adults, is largely unknown, and the relative importance of these two dispersal stages is probably species-specific (Schiel 2004, Schiel and Foster 2006).

Dispersal by propagules

Many species release propagules such as gametes or spores into the surrounding water column. Due to their microscopic size and the viscous medium into which they are released, dispersal is then controlled largely by substratum topography, hydrodynamic conditions, and the length of time the propagules remain in the water column (Santelices 1990, Amsler *et al.* 1992, Norton 1992, Johnson and Brawley 1998). Propagule characteristics such as size, density and behaviour, in conjunction with the height of release above the substratum, affect the amount of time propagules remain in suspension, and thus their potential for dispersal (Santelices 1990, Amsler *et al.* 1992, Norton 1992). Dispersal is also influenced by the size of the source population, and the synchronous release of gametes or spores. A large adult population that synchronizes the release of propagules can have a larger spore shadow, and thus higher dispersal potential, due to reduced effects of dilution and diffusion (Anderson and North 1966, Hoffmann 1987, Norton 1992, Reed *et al.* 1997, Reed *et al.* 2004). In general, however, long distance dispersal by algal propagules is thought to be relatively limited (Anderson and North 1966, Dayton 1973, Deysher and Norton 1982, Kendrick and Walker 1991, Lu and Williams 1994, Williams and Difiori 1996, Serrao *et al.* 1997, Kinlan and Gaines 2003).

Motile spores, such as those released by laminarian algae, may have the greatest potential to disperse, but even these are likely to act as passive particles at scales greater than a few millimetres in typical water conditions (Graham 2003). Laminarian spores are generally only ~6-10μm in length (Schiel 2004) and maximum swimming speeds are ~80-300μms^{-1}, whereas wave driven flows are typically 1-10ms^{-1} (Norton 1992). Therefore, although spore motility may be useful for settlement after release from the adult plant, it is probably insignificant as a dispersal mechanism, and spores are likely to be transported passively in ocean currents (Norton 1992, Schiel and Foster 2006).

Dispersal by spores is generally thought to be limited to a few meters (Anderson and North 1966). However, most information on dispersal estimates has come from studies focused on recruitment (Anderson and North 1966, Dayton 1973, Hruby and Norton 1979, Deysher and Norton 1982, Vandermeulen and DeWreede 1986, Arrontes 2002). These can be underestimates of dispersal because microscopic zygotes and spores can suffer significant mortality after settlement, before successfully recruiting to a population (Norton 1992). Recent studies have shown spores may disperse several kilometres. For example, Gaylord *et al*. (2002) showed that propagules of the giant kelp *Macrocystis pyrifera* can disperse more than 1km. However, the decline in density with distance from source populations may prevent successful fertilisation and subsequent recruitment. Reed (1990) found that a minimum settlement density of 1 spore mm^{-2} was necessary for the recruitment of *M. pyrifera*, which may be determined by the maximum distance separating male and female gametophytes at which successful fertilisation is possible.

Fucoid algae are generally thought to have very limited dispersal potential because there is no obligate planktonic stage, and they have relatively large (>30µm), non-motile, negatively buoyant eggs and zygotes (Kendrick and Walker 1991, Chapman 1995, Kendrick and Walker 1995, Johnson and Brawley 1998, Schiel and Foster 2006). Furthermore, some species release their gametes during periods of calm water (Serrao *et al.* 1996, Pearson *et al.* 1998) which may also restrict their dispersal. Dispersal estimates for fucoids are typically less than 30m, with an exponential decline in densities with distance (Sousa 1984, Kendrick and Walker 1991, Chapman 1995, Kendrick and Walker 1995, van-Tamelen *et al.* 1997, Johnson and Brawley 1998, Dudgeon *et al.* 2001, Bellgrove *et al.* 2004).

Successful recruitment may also be density-dependent for some fucoids (reviewed in Schiel and Foster 2006). High densities of recruits may be required for viable adult populations to form due to reductions in heat, desiccation stress, and grazing (Schonbeck and Norton 1978, Hruby and Norton 1979, Ang and DeWreede 1992). Furthermore, for dioecious species, there may be a specific distance separating male and female gametes, and a minimum concentration of sperm (Berndt *et al.* 2002), required for successful fertilisation. Therefore, it is unlikely that the long-distance dispersal of marine algae occurs via propagules alone.

Dispersal by drifting adults

The relatively short-range dispersal of propagules may be extended by the detachment and drift of reproductive adult plants. Macroalgae frequently become detached from the primary substratum as a result of physical or biological disturbances such as grazing by herbivores, or storms (Dayton *et al.* 1992), and may travel considerable distances in open ocean currents. The trans-oceanic distributions of invertebrate species, with short lived larval stages, are most likely a result of long-distance rafting events (Donald *et al.* 2005). Similarly, most long-distance dispersal in seaweeds is thought to occur via drifting plants, or fertile plant fragments, that have become detached from the substratum and are transported by prevailing currents (van den Hoek 1987).

Drift algae has been observed in surface waters all over the world, and often far from the nearest source population (reviewed in Thiel and Gutow 2005a). For example, Smith (2002) estimated that over 70 million rafts of *D. antarctica* are adrift at any one time in the Southern Ocean, with the nearest probable source population to the west up to 5000km away. Many fucoids, and some laminarians, have buoyant adult fronds, allowing detached plants to drift on the sea surface to distant sites and, if they are reproductively active, subsequently release their gametes or spores (Hoffmann 1987, Santelices 1990). At least some species of drifting algae can continue to grow and maintain positive buoyancy for weeks or months after detachment, and can even form reproductive structures and become fertile while drifting (Norton 1981, van den Hoek 1987, Norton 1992, Hobday 2000a, 2000b, Vandendriessche *et al.* 2007). Detached adult plants can, therefore, provide the potential for large-scale dispersal and population connectivity.

Evidence of the effectiveness of drifting as a viable long distance dispersal mechanism comes from the extensive geographic distribution of many algal species, when distances between populations and the potential source locations are beyond the dispersal range of algal propagules (van den Hoek 1987). Phylogeographic studies have found a low degree of genetic structure between populations of *Fucus spiralis*, suggesting long-range dispersal events increase gene flow (Coleman and Brawley 2005). Species within the *Macrocystis* genus show very little genetic variation (Coyer *et al.* 2001), and it has been suggested that the amphitropical distribution of *M. pyrifera* resulted from the long-distance dispersal of drifting viable sporophytes (North 1972, Nicholson 1978, Lindberg 1991). Moreover, the rapid spread of the invasive fucoid *Sargassum miticum* has also been attributed to dispersal by detached, drifting reproductive fragments (Fletcher 1980, Deysher and Norton 1982, Fletcher and Callow 1992). Such dispersal distances range from hundreds to thousands of kilometres. However, this evidence carries with it the assumption that not only has drifting macroalgae travelled long distances after detachment from the substratum but that successful colonisation has occurred at a new and distant location (Thiel and Gutow 2005a).

The successful long-distance dispersal of drifting algae and subsequent colonisation at a distant site depend on several factors, including the longevity of the drifting algae, specifically the ability to float and maintain buoyancy, the reproductive longevity of drifting algae and drift algae that has been cast onshore (beach-cast), and the ability to move offshore after detachment and back onshore at a new and suitable habitat. Furthermore, successful fertilisation and recruitment are required after arrival at a new and distant site. These factors will be influenced by nearshore processes and species characteristics and, therefore, marine algae may differ in their potential for long distance dispersal by drifting. However, despite the apparent acceptance of drifting adults as a long-distance dispersal mechanism, very little is known about the relative potential of drifting adult plants to be a viable long-distance dispersal mechanism, and how the ability to disperse by drifting varies between species. Furthermore, most studies have been on large subtidal algae, such as *Macrocystis* (Harrold and Lisin 1989, Hobday 2000a, 2000b, Macaya *et al.* 2005, Hernandez-Carmona *et al.* 2006). Intertidal algae that are not continually submerged may have far different growth and reproductive characteristics once set adrift in open waters.

Dispersal by drifting may be highly episodic and, therefore, not very effective for most species (van den Hoek 1987). Reproductive activity of drifting plants may be significantly reduced and, even if viable gametes are released, they may be too diffuse for eggs of dioecious species to be fertilised. Even then, reduced settlement densities may result in high mortality and low recruitment. Furthermore, detached algae may be immediately beach-cast high on the shore, reducing the probability of dispersal to new sites. Therefore, it is important to understand the characteristics of drifting algae, and the influence of nearshore processes on the dispersal of drift, in order to understand the ecological importance of drifting as a long-distance dispersal mechanism.

Fucoid algae

Fucoid algae have intrinsic differences in their life history characteristics that can influence how they interact with the nearshore environment, and their subsequent dispersal, settlement and recruitment. Fucoids are either monoecious or dioecious, and this can influence fertilisation success and the genetic structure of populations (Brawley and Johnson 1992). Reproductive activity also varies temporally among species (Hoffmann 1987, Brawley and Johnson 1992). Some species are reproductive throughout the year, with larger pulses of reproductive activity in certain months, while others are seasonally reproductive (Taylor and Schiel 2003, Schiel and Foster 2006). This can influence succession and competitive interactions after disturbance (Sousa 1979, Santelices 1990), dispersal and recruitment success. Environmental conditions that are favourable for dispersal are unimportant if species are unable to release viable propagules at appropriate times. Furthermore, although most fucoids are at least potentially capable of dispersing as drifting adults, not all float in the surface waters when detached. Therefore, because the movement of drift material is primarily influenced by the movement of the water in which it floats, the position of the algae in the water column may play an important role in the movement of drift, and subsequently influence dispersal.

Fucoids are dominant occupiers of primary space in the middle to low intertidal zone along the eastern coast of southern New Zealand (Schiel 2004, 2006, Schiel and Foster 2006). The large southern bull kelp, *Durvillaea antarctica*, dominates wave-exposed shores, and smaller fucalean algae, such as *Cystophora torulosa* on the lower shore, and *Hormosira banksii* on the mid-shore, dominate more sheltered sites. All three species rely on external fertilisation, have simple life cycles (no alternation of generations), and have no obligate planktonic developmental stage. A diploid adult releases relatively large, non-motile haploid eggs and motile sperm that, following fertilisation, develop into diploid juveniles that grow directly into adults. Fertilisation and attachment usually occur within a few hours of gamete release (Brawley *et al.* 1999). These characteristics facilitate studies of dispersal, settlement and recruitment (Chapman 1995, Johnson and Brawley 1998).

D. antarctica, *H. banksii* and *C. torulosa* make up a significant portion of coastal drift and beach-cast seaweed along the coast of southern New Zealand. Drifting *D. antarctica* has been reported to dominate the floating algal species in the Southern Ocean (Smith 2002), and is frequently cast ashore in regions it does not grow (e.g. the Kermadec islands) (Adams 1994). Similarly, drifting *H. banksii* has been recorded to be transported by currents, and cast ashore at distant sites (Adams 1994). However, very little is known about the potential importance of drifting as a long distance dispersal mechanism for these species, or about their reproductive biology after detachment. They are key species that drive diversity (Schiel 2006) and an understanding of their potential for short and large-scale dispersal is essential for understanding community recovery, and population dynamics in the face of anthropogenic influences (Schiel 2004).

1.1 Study aims

This thesis tests hypotheses about the ability of habitat-forming intertidal fucoid algae to disperse as reproductively viable adults. For drifting to be a viable mechanism of long-distance dispersal, it requires the successful completion of several key processes. The ability to disperse and release viable gametes at a new and distant location largely depends on the ability of algae to remain functionally reproductive following detachment. Chapter 2 examines the reproductive viability of drifting and beach-cast algae. The reproductive activity and viability of drifting and beach-cast plants are compared to control plants, which remain attached to the substratum. I test the hypotheses that reproductive activity is not significantly reduced over time after detachment from the shore, that released propagules continue to be viable, and that there is no difference in reproductive viability between treatments (drifting, beach-cast, and controls).

The relative success of drifting algae as a long-distance dispersal mechanism also depends on the ability of drift to move offshore, out of the turbulent nearshore environment, following detachment. Chapter 3 investigates the influence of nearshore processes on the movement of fucoid algae after detachment. The conditions favourable for both retention and dispersal offshore are examined, to test the hypothesis that wind-induced and tidal currents do not influence the movement of drifting algae, and that there is no difference in the movement of drift between algal species, or the release location in the tidal zone (low, mid and high shore).

Chapter 4 then investigates the proximity between male and female gametes of dioecious species required for successful fertilisation. This chapter tests the hypothesis that the distance between male and female gametes does not influence fertilisation success. The ability of monoecious species to self-fertilise, and the longevity of sperm after release from an adult plant is also tested. The potential for the long-distance dispersal of fucoid algae by drifting adult plants is discussed in Chapter 5.

1.2 Study areas

Kaikoura Peninsula

The Kaikoura Peninsula (42° 25' S, 173° 44' E) is situated on the north-east coast of the South Island of New Zealand (Fig. 1.2). The peninsula is narrow, and projects approximately four kilometres out to sea. The continental shelf is only 4-5km wide and, within one kilometre of the coast, the Kaikoura Canyon reaches depths of over 1000 meters, with depths of over 2300 meters approximately 20 kilometres offshore (Rasmussen 1965).

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, Winterbourn *et al.* 2008). The peninsula is located at the northern end of the Southland Current, which then deflects offshore over the Chatham rise (Heath 1985), where the cooler subantarctic waters mix with the warmer subtropical waters of the East Cape Current (Heath 1985). Fluctuating subtropical and subantarctic oceanic influences, combined with the significant inputs from rivers north and south of the peninsula, cause large variations in the characteristics of the surrounding nearshore water mass. Currents, bottom topography, and wind, contribute to the upwelling of cold water, which occurs in regular pulses throughout the year, and sea-surface temperatures in this area range between 9-18°C (Chiswell and Schiel 2001).

Rocky shores around the Kaikoura Peninsula exhibit varying substrate, topography, and exposure to wave action. The majority of the intertidal platforms are composed of mudstone and limestone, and are mostly algal-dominated. However, mussels and barnacles are common on Greywacke outcrops north and south of the peninsula. On the high shore, extensive rocky intertidal platforms are dominated by bare space and grazers with some ephemeral algae, while in lower zones there is an abundance of fucoid algae. The coastline is subjected to a wide range of exposures to wave action, which can influence the distribution and abundance of intertidal species (Morton and Miller 1968, Schiel and Taylor 1999, Taylor and Schiel 2003). Many of the intertidal platforms are sheltered from oceanic swells through their aspect and the presence of headlands. Sheltered sites (e.g. Wairepo Flats) are dominated by *Hormosira banksii* (on the mid-shore) and *Cystophora spp.* (on the lower shore). Exposed sites (e.g. Seal Reef and Oaro) are subjected to strong oceanic swells resulting from winds that are predominately south and southeast in winter and northeast in summer (Rasmussen 1965). The large southern bull kelp *Durvillaea antarctica* dominates the lower shore at exposed sites.

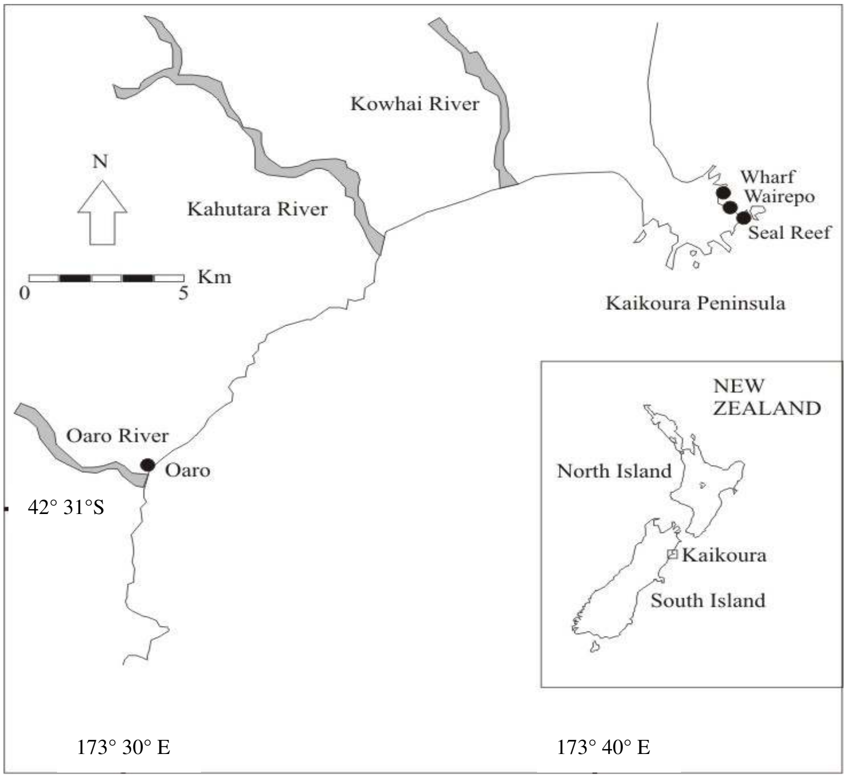


Figure 1.2: Map of the Kaikoura Peninsula showing study areas (Wairepo, Seal Reef, Oaro), the location of 'the wharf' used for experiments in Chapter 2, and the location of Kaikoura Peninsula on the east coast of the South Island of New Zealand.

1.3 Study species

Hormosira banksii

Hormosira banksii (Turner) Descaisne (Fig. 1.3) is a perennial fucoid alga that dominates the middle to lower shore on many sheltered or moderately-exposed platforms throughout New Zealand and southern Australia. *H. banksii* is a dioecious species that is reproductive throughout the year (Osborn 1948), but there are large pulses in reproduction during the warmer months (September- January) (Taylor and Schiel 2003). Branches consist of small, buoyant, fluid-filled bladders or nodes, which protect against heat and desiccation stress at low tide (Brown 1987). Male and female gametes are produced in conceptacles located near the surface of the nodes. When mature, females release four pale green eggs per oogonium, and males release bright orange sperm (Adams 1994).

Figure 1.3: Picture of *Hormosira banksii* tagged with cable ties for experiments done in Chapter 2.

Durvillaea antarctica

Durvillaea antarctica (Chamisso) Hariot, or southern bull kelp (Fig. 1.4a), has a wide circumpolar distribution in the cooler waters of the southern hemisphere. It is common at low water on exposed reefs throughout New Zealand, the Subantarctic Islands, and the southern South American coasts of Chile and Argentina (Adams 1994). Large, flat, leathery blades arise from a single unbranched stipe, and these are buoyant due to an internal gas-filled honeycomb tissue (Adams 1994). *D. antarctica* is a dioecious species and is reproductive from May to August (late autumn through winter) (Clayton 1990, Taylor and Schiel 2005). Males produce motile sperm and females produce larger, non-motile eggs, which are expelled in packets of four in a sticky mucilage. Gametes are released from raised conceptacles, which are located over the entire blade surface (Adams 1994).

Cystophora torulosa

Cystophora torulosa (R. Brown) J. Agardh (Fig. 1.4b) is a perennial fucoid alga that dominates the low intertidal and immediate subtidal zones on semi-sheltered reefs over much of the coast of New Zealand. Plants grow to approximately 60cm and have a tough main stipe, from which clusters of lateral branches arise (Adams 1994). In contrast to *H. banksii* and *D. antarctica*, plants are monoecious, producing one egg per oogonium. *C. torulosa* is reproductive from late spring through summer.

(a)

(b)

Figure 1.4: Pictures of *Durvillaea antarctica* (a) and *Cystophora torulosa* (b) tagged with cable ties for experiments done in Chapter 2.

Chapter 2 -Reproductive Viability and Abundance of Drifting Fucoid Algae

2.1 Introduction

The ecological importance of drifting in different regions will depend on the abundance of drifting algae (Thiel and Gutow 2005a), and whether this drift is reproductively viable. There have been numerous quantitative assessments of drifting algal abundance throughout the world (Kingsford and Choat 1986, Kingsford 1992, Hobday 2000a, Smith 2002), but few have determined if this drift is reproductively active. Evidence supporting drifting as a method of long-distance dispersal comes from the extensive geographic range and distribution of populations, that may be separated by large areas of coastline or ocean basins (Coyer *et al.* 2001, Smith 2002, Waters 2008), the recovery of populations following disturbances (Vega *et al.* 2005), and the rapid spread of invasive species (Fletcher 1980, Deysher and Norton 1981, Fletcher and Callow 1992), all in the absence of a local source within the dispersal range of gametes or spores (van den Hoek 1987). However, the spatial scale over which long-distance dispersal can effectively occur largely depends on the reproductive longevity of drifting algae following detachment, and little is know about the ability of algae continue to reproduce while adrift, or as beach-cast material after deposition on the shore.

Some of the first experimental evidence that detached algae may remain functionally reproductive while drifting was obtained from floating rafts of *Macrocystis pyrifera.* Macaya *et al*. (2005) found 26.8% of sporophytes sampled at nine locations along the coast of Chile possessed sporophylls with sori containing sporangia. Furthermore, the drifting sporophytes released viable zoospores. They concluded that reproductive viability could be maintained for at least 21 days because of the size of attached stalked barnacles (*Lepas spp.*). Hernandez-Carmona *et al*. (2006) further investigated the reproductive longevity of drifting *M. pyrifera* by tethering sporophytes to surface buoys and assessing reproductive viability every 5-16 days. Drifting sporophytes remained reproductively viable as long as sori were present (125 days). However, with the exception of these studies, few have tested whether drift and beach-cast algae are functionally reproductive, and within these studies large brown fucoid algae are poorly represented (Schiel and Foster 2006).

Drifting and beach-cast fucoid algae are abundant along the southern coast of New Zealand, but the reproductive viability of this drift has never been tested (Schiel 2004). Some of the highest abundance estimates of drifting algae have been obtained from the coastal waters of northern New Zealand (Kingsford 1992), but the abundance of drift is unimportant for the dispersal potential of marine algae if they are not reproductively active. This chapter tests the functional reproductive longevity of three species of drifting and beach-cast fucoid algae: *Hormosira banksii*, *Durvillaea antarctica* and *Cystophora torulosa*. To test the reproductive dynamics of fucoid algae after detachment, the reproductive activity of drifting and beach-cast algae was compared to attached, onshore populations. I also tested whether the propagules that were released were viable. Furthermore, transect surveys were used to investigate the abundance, species composition, and reproductive status of drifting algae around two peninsulas on the east coast of the South Island of New Zealand.

2.2 Methodology

Reproductive longevity and viability of drifting and beach-cast algae

To test the reproductive longevity of drifting and beach-cast algae, a series of experiments were done during the winter of 2007 (for *H. banksii* and *D. antarctica*) and during the spring and summer of 2007 and 2008 (for *H. banksii* and *C. torulosa*). In each experiment, 10 replicates of two treatments (drifting and attached controls for drifting experiments, and beach-cast and attached controls for beach-cast experiments) were tested for reproductive viability (Fig. 2.1).

Each replicate consisted of 10 reproductive plants that were tagged in the field (Wairepo Reef for *H. banksii* and *C. torulosa*, and Oaro and Seal Reef for *D. antarctica*) using cable ties. For the 'Drifting' and 'Beach-cast' treatments, one large frond was removed from each of the attached plants and placed in a mesh bag (10 fronds per bag). For the drifting experiments, 10 mesh bags, each containing 10 fronds from the tagged attached plants, were then attached to a rope with cable ties. The rope was then tied to a wharf at Kaikoura to simulate drifting, yet allowing for regular sampling. Bags that contained buoyant species (*H. banksii* and *D. antarctica*) floated within the surface waters, whereas *C. torulosa* did not float on the surface, and bags sat lower in the water column. For the beach-cast experiments, 10 mesh bags were attached to a rope with cable ties, and one end of the rope was tied to a tree on the high shore, ensuring the bags were free to move with the naturally beach-cast material on the high tide mark. The remaining portions of the plants were left attached to the shore and were sampled as attached controls. Each experiment, therefore, involved 100 plants attached on the shore and 100 fronds of drifting or beach-cast plants. Drifting and beach-cast experiments were repeated 4 times for each species.

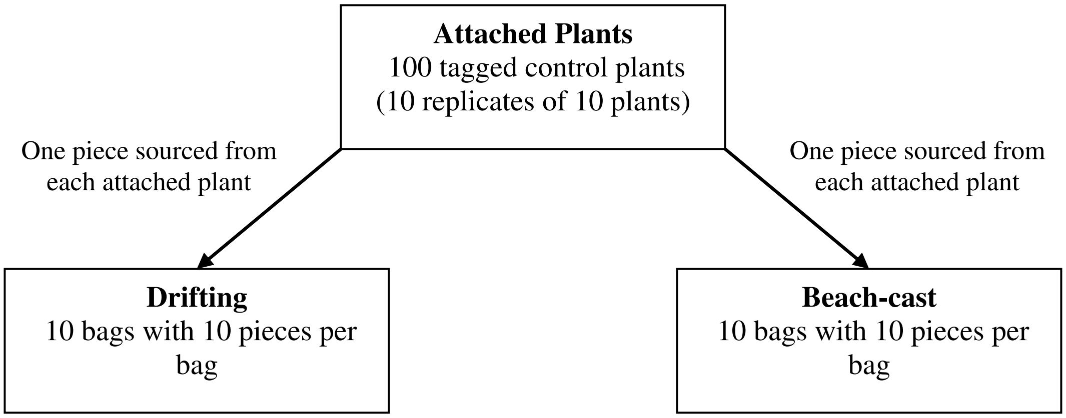


Figure 2.1: Diagram showing the experimental design for comparing reproductive longevity and viability of attached control algae versus drifting and beach-cast pieces from the same plants. Pieces of algae were removed from 100 "attached plants" (10 replicates of 10 plants), which were tagged and remained attached to the substratum as controls. Algal pieces were then placed in mesh bags (10 bags for each treatment and 10 pieces of algae per bag) and tied to a wharf to simulate drifting, or tethered at the high tide line on the shore to simulate being beach-cast.

To sample reproductive viability, small pieces of seaweed, with an average blotted wet weight of 16.4g ± 5.1 ($\bar{x}$ ± s.e) for *H. banksii*, 34.02g for *D. antarctica* and 30.74g for *C. torulosa*, were removed from the fronds in the experimental treatments after 0, 1, 3, 7, 14, 21, 28 and 35 days. The final sampling day for *H. banksii* was day 57, *D. antarctica*, day 62, and *C. torulosa* day 43. Samples from each replicate bag, or group of attached control plants, were placed in separate containers (one container for each replicate) and refrigerated at 4°C for 24 hours.

Standard gamete release methods were used (e.g., Taylor and Schiel 2003). To stimulate gamete release, samples were exposed to light at room temperature for 30 minutes before they were immersed in 500ml of filtered seawater. Algae were then agitated to wash gametes from the samples. The resulting gamete mixture was then left for 15 minutes to allow fertilisation to occur, before being poured over 10 x 10cm fibrolite (‘Hardiflex™’) plates, which provided a standard substratum on which the microscopic zygotes could settle and attach. Fibrolite plates were soaked in seawater for 12h prior to the settlement.

To monitor reproductive output, a dissecting microscope was used to count the number of propagules in ten random 1cm^2 squares on each plate (settled propagules). To test if settled propagules were viable, settled plates were then left for 24 hours before they were washed vigorously with seawater. Following washing, the same ten 1cm^2 squares were examined, and the number of firmly ‘attached’ propagules was counted. After 48 hours, attached viable zygotes were easily distinguished from unfertilised non-viable eggs as they had elongated. Following gamete release, the pieces of algae in each replicate were weighed, and total propagule abundance was estimated as the number of propagules settled and attached (viable) cm^{-2} g^{-1} of algae. This was then multiplied by 100, to get the number of propagules settled and attached (viable) cm^{-2} 100g^{-1} of algae, which was then used for all analyses.

Data were analysed using a two way analysis of variance (ANOVA) in which days were treated as a random factor. Prior to ANOVA, data were square-root or log (n+1) transformed to stabilise variances. In some cases variances could not be stabilised through transformation. In these cases, the significance level was increased to 0.01 to reduce the probability of Type I errors (Quinn and Keough 2002).

Species composition, abundance, and reproductive status of drift

To provide an estimate of drifting algal abundance and species composition, drifting algae were surveyed by boat in the nearshore waters around Kaikoura and Banks Peninsula. Five 2km transects were done at each location (Kaikoura and Banks) in June 2007. Transect start points were randomly selected at points c.500m from shore, and a direct heading was plotted. Each piece of drift material within 5m of either side of the transect line was collected, its location marked using a hand-held Garmin Etrex™ Global Positioning System (GPS), and placed in a plastic zip lock bag. Bags were then placed in a large plastic bin containing ice for later analysis.

In the laboratory, drift algae were weighed wet and the reproductive status was determined by examination of reproductive structures, and by microscopic examination of transverse fine sections of conceptacles on the blades, fronds or nodes.

For comparison with other studies, abundance and biomass estimates were obtained by multiplying the average number and biomass of drifting algae collected within the 5 transects (transect length x transect width x the number of transects), by 10.

Additionally, in August 2007, several large *D. antarctica* with stalked barnacles (*Lepas anatifera*) on their holdfasts and fronds were beach-cast on Wairepo Reef, Kaikoura. Samples of barnacles were removed, and the length of the scutum was measured. Stalked barnacles have been used to estimate drifting times because they are found attached to floating substrata, and scutum size can accurately indicate minimum floating time (Thiel and Gutow 2005b). Reproductive viability was determined by transverse sections of the fronds and microscopic examination for gametes.

2.3 Results

Reproductive longevity and viability of drifting and beach-cast algae

Longevity

Drifting algae

Drifting algae released propagules for the duration of the experiments (*H. banksii* 57 days, *D. antarctica* 62 days, and *C. torulosa*, 43 days) (Fig 2.2). The number of propagules released from drifting treatments was not significantly different from the number of propagules released from attached controls for any of the three study species (Table 2.1): *H. banksii* ($F_{1,220} = 3.71$, $p = 0.90$), *D. antarctica* ($F_{1,98} = 1.78$, $p = 0.22$), *C. torulosa* ($F_{1,178} = 4.41$, $p = 0.17$). However, for *C. torulosa*, this depended on the day monitoring occurred (day x treatment interaction, $F_{12,178} = 3.61$, $p<0.001$), due to significantly fewer propagules being released from drifting algae on days 35 and 43 (Tukey HSD, $p < 0.01$). Therefore, the reproductive activity of detached *H. banksii* and *D. antarctica* was not reduced while drifting, and was no different to algae that remained onshore and attached to the substratum. However, drifting *C. torulosa* released significantly fewer propagules on the last two sampling days.

Reproductive activity was variable for both drifting and attached *H. banksii* and *C. torulosa*, with a significant difference in the number of propagules released between sampling days: *H. banksii* ($F_{8,220}=3.67$, $p<0.001$) and *C. torulosa* ($F_{12,178} = 4.40$, $p<0.001$).

Table 2.1: ANOVA on the number of zygotes settled cm^{-2} $100g^{-1}$ of drifting and attached *Hormosira banksii* to day 57 (a), *Durvillaea antarctica* to day 62 (b), and *Cystophora torulosa* to day 43 (c). [1]Cochrans test was significant. [2] Data were log $_{(n+1)}$ transformed and Cochrans tests not significant.

Effect	df	MS	F	p
(a) ***H. banksii***[1]				
Day	8	35.331	3.673	**0.000**
Treatment	1	18.654	3.708	0.090
Day x Treatment	8	5.030	0.523	0.838
Error	220	9.618		
(b) ***D. antarctica*** [2]				
Days	7	12.918	1.241	0.287
Treatment	1	5.267	1.780	0.223
Day x Treatment	7	2.958	0.284	0.958
Error	98	10.405		
(c) ***C. torulosa***[1]				
Day	12	3.186	4.408	**0.000**
Treatment	1	5.465	2.094	0.173
Day x Treatment	12	2.609	3.610	**0.000**
Error	178	0.722		

Beach-cast algae

No propagules were released from beach-cast *H. banksii, D. antarctica* or *C. torulosa* when sampled at day 14 (Fig. 2.2). Therefore, to compare the reproductive activity of beach-cast algae with drifting and control plants, two way ANOVAs were done using beach-cast, drifting, and control data up to day 7 (Table 2.2).

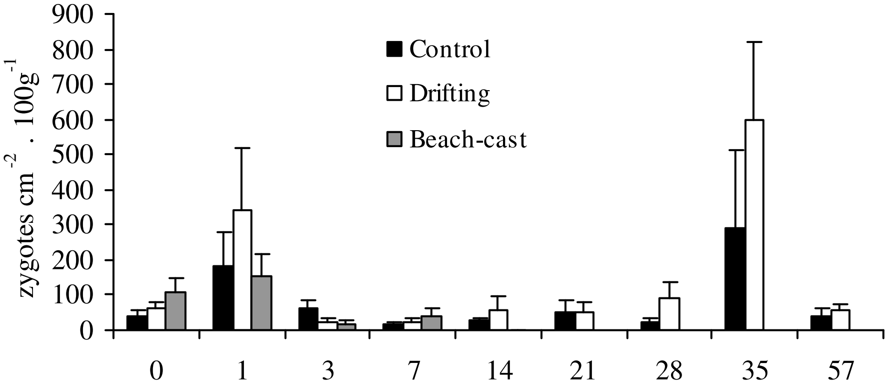
For *H. banksii*, there was no difference in the number of propagules released from beach-cast, drifting, and control algae, up to day 7: *H. banksii* ($F_{2,6}$ = 2.76, p = 0.13). However, beach-cast *D. antarctica* released significantly fewer propagules on day 7, (Tukey HSD, p <0.001) and there was a significant interaction effect (day x treatment interaction, $F_{6,118}$ = 4.19, p<0.001). Apart from day 7 beach-cast *D. antarctica*, the reproductive activity of beach-cast *H. banksii* and *D. antarctica* was maintained at levels similar to attached controls, but by day 14 beach-cast algae were no longer reproductively active.

In contrast, for *C. torulosa* there was a significant difference in the reproductive activity of beach-cast algae compared to drifting algae and attached controls ($F_{2,6} = 6.31$, $p < 0.05$), due to consistently lower settlement from beach-cast *C. torulosa* (Tukey HSD, $p < 0.001$). As with *H. banksii* and *D. antarctica*, no propagules were released from beach-cast *C. torulosa* when sampled after 14 days.

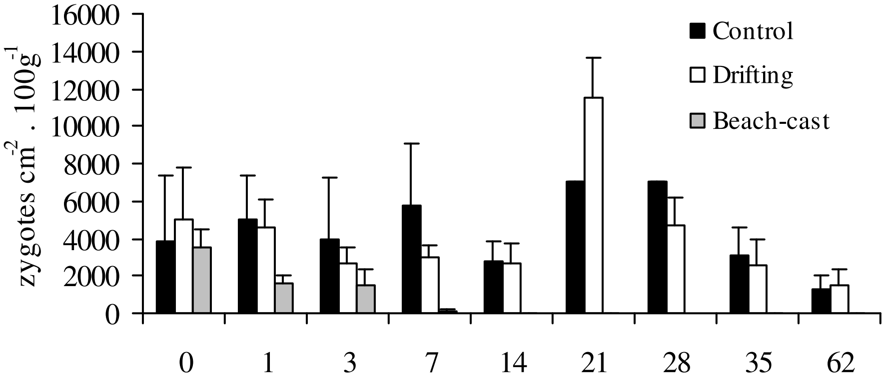
Table 2.2: ANOVA on the number of zygotes settled cm^{-2} 100g^{-1} of beach-cast, drifting, and attached *Hormosira banksii* (a), *Durvillaea antarctica* (b) and *Cystophora torulosa* (c) to day 7.
[1] Cochrans test was significant. [2] Data were $\log_{(n+1)}$ transformed and Cochrans tests not significant.

Effect	**df**	**MS**	**F**	**p**
(a) *H. banksii*[2]				
Day	3	4.842	1.840	0.233
Treatment	2	7.224	2.762	0.130
Day x Treatment	6	2.652	1.193	0.314
Error	125	2.222		
(b) *D. antarctica* [1]				
Days	3	31.282	2.070	0.205
Treatment	2	23.195	1.556	0.284
Day x Treatment	6	15.207	4.194	**0.000**
Error	118	3.625		
(c) *C. torulosa*[1]				
Day	3	28167	2.965	0.117
Treatment	2	58976.7	6.306	**0.029**
Day x Treatment	6	9551.6	1.510	0.178
Error	138	6322.3		

(a) ***Hormosira banksii***



(b) ***Durvillaea antarctica***



(c) ***Cystophora torulosa***

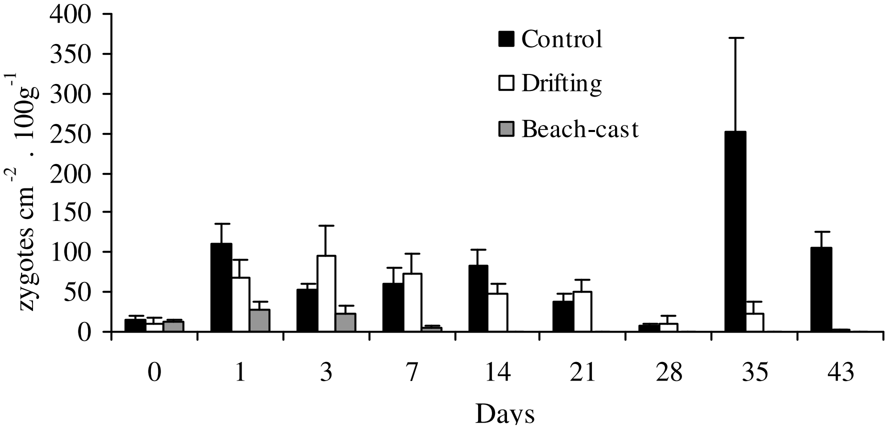


Figure 2.2: Graphs showing the number of zygotes settled cm^{-2} $100g^{-1}$ (+1s.e.) from experimental control, drifting and beach-cast *Hormosira banksii* (a), *Durvillaea antarctica* (b), and *Cystophora torulosa* (c) over time.

Viability

All three species continued to release viable propagules throughout the experiments when drifting (*H. banksii* 57 days, *D. antarctica* 62 days and *C. torulosa* 43 days), and when beach-cast (up to 7 days) (Fig 2.3). Simple linear regression analysis and ANOVA were used to test the relationship between settled and attached (viable) zygotes. There was a significant positive linear relationship between the number of propagules released (settled), and the number propagules that were viable (attached) for *H. banksii*, *D. antarctica* and *C. torulosa*, over all treatments (controls, drifting and beach-cast) (Fig 2.4). For *H. banksii* and *D. antarctica* there was almost a 1:1 ratio of settled to attached propagules. For *C. torulosa*, this relationship was more variable.

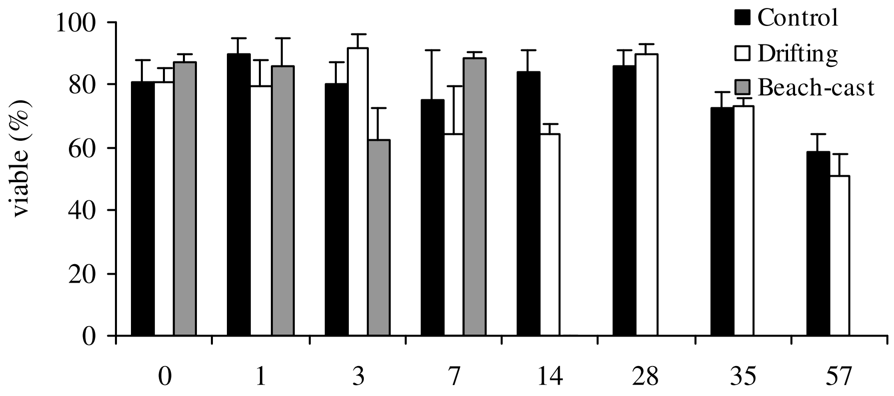
Drifting algae

The percentage of viable propagules released from drifting algae was not significantly different from that released from attached controls, for all three species (Table 2.3): *H. banksii* ($F_{1,150} = 0.60$, $p = 0.46$), *D. antarctica* ($F_{1,101} = 0.52$, $p = 0.48$), *C. torulosa* ($F_{1,144} = 0.15$, $p = 0.70$). There was a significant difference in the percentage of viable propagules released between sampling days for *D. antarctica* ($F_{7,101} = 9.65$, $p<0.001$), due to significantly lower viability on days one and seven (Tukey HSD, $p<0.01$). However, this difference was evident in drifting and control treatments, so was independent of being detached and adrift. Therefore, viability was not significantly reduced when drifting for all three study species, and was not significantly different from attached algae on the shore.

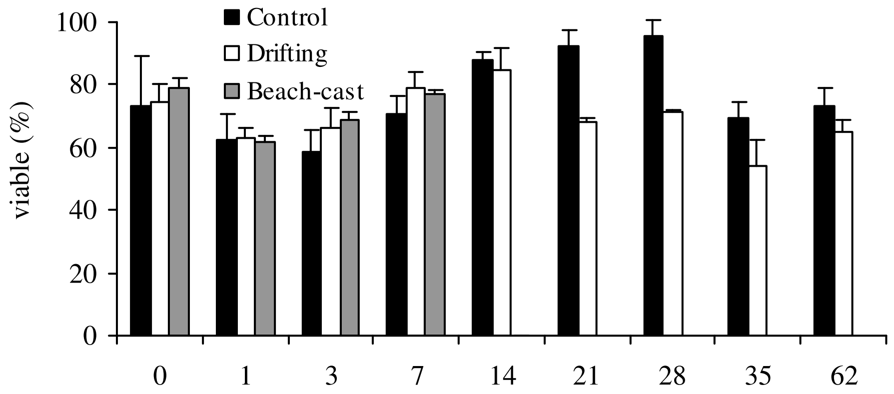
Beach-cast algae

Viability was also not significantly reduced in algae that were beach-cast, at least to 7 days. However, the percentage of viable propagules released from beach-cast algae differed between days for *D. antarctica* and *C. torulosa* (Table 2.3). On some days the percentage of viable propagules released from beach-cast *D. antarctica* (day 0 and 3, Tukey HSD, $p<0.01$) and *C. torulosa* (day 1, Tukey HSD, $p<0.01$) was greater than that of drifting and attached plants, causing a significant interaction effect: *D. antarctica* ($F_{6,118} = 4.19$, $p<0.05$), and *C. torulosa* ($F_{6,138} = 2.27$, $p<0.05$).

(a) ***Hormosira banksii***



(b) ***Durvillaea antarctica***



(c) ***Cystophora torulosa***

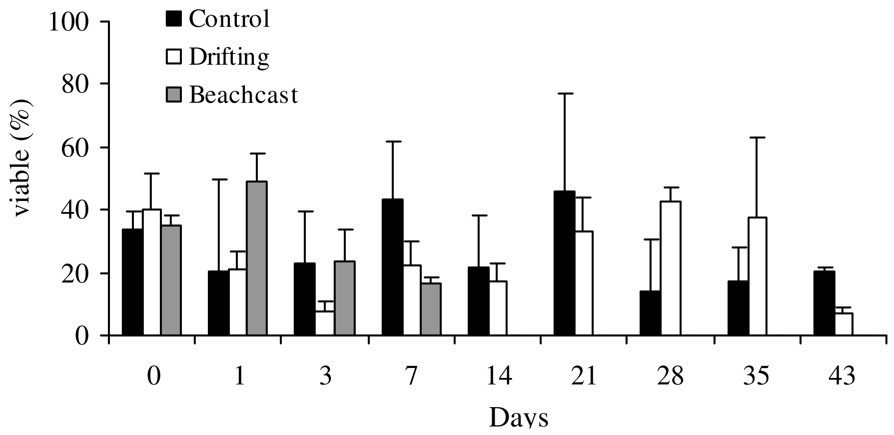
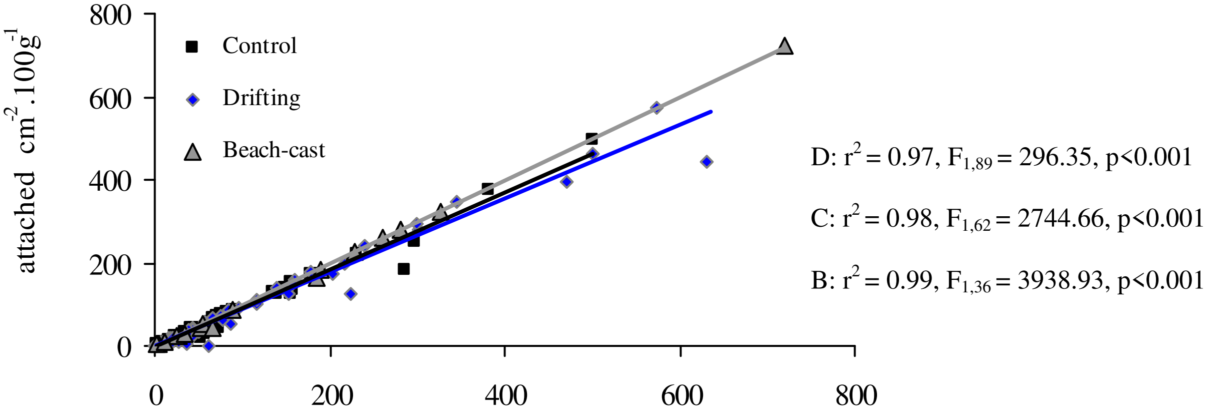
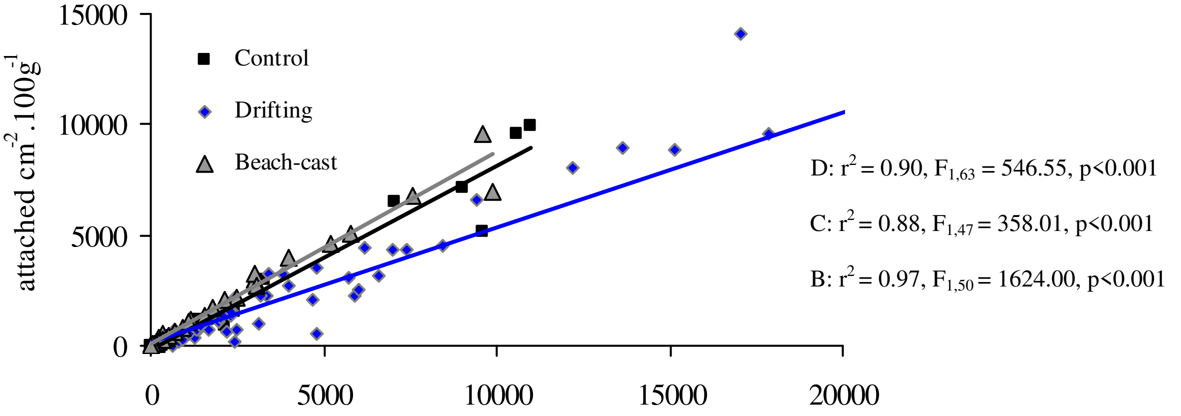


Figure 2.3: The percentage of viable zygotes cm^{-2} 100g^{-1} (+1s.e) from experimental attached (control), drifting and beach-cast *Hormosira banksii* (a), *Durvillaea antarctica* (b) and *Cystophora torulosa* (c).

(a) *Hormosira banksii*



(b) *Durvillaea antarctica*



(c) *Cystophora torulosa*

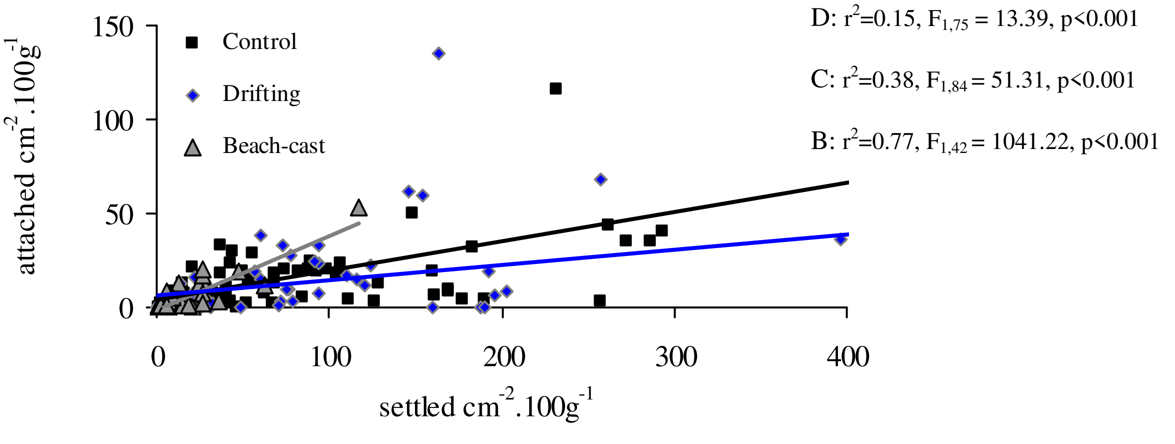


Figure 2.4: Average number of zygotes cm^{-2} 100g^{-1} settled (released) against the number of zygotes attached (viable) from experimental drifting, control and beach-cast *Hormosira banksii* (a), *Durvillaea antarctica* (b), and *Cystophora torulosa* (c). Simple linear regression was used to test the relationship between settled and attached (viable) zygotes. D = Drifting, C = Control and B = Beach-cast.

Table 2.3: Two-way ANOVA on the percentage of viable propagules (attached) cm^{-2} $100g^{-1}$ released from drifting algae and attached controls, and beach-cast, drifting, and control algae to day 7 for *Hormosira banksii* (a,b), *Durvillaea antarctica* (c,d) and *Cystophora torulosa* (e,f). All Cochran's tests were significant.

Effect	**df**	**MS**	**F**	**p**
(a) *H. banksii* (Drift and control to day 57)				
Day	6	2016.7	2.7026	0.126
Treatment	1	450.2	0.5986	0.463
Day x Treatment	6	746.2	0.9311	0.474
Error	150	801.5		
(b) *H. banksii* (All treatments to day 7)				
Day	3	473.4	0.425	0.742
Treatment	2	84.4	0.077	0.927
Day x Treatment	6	1128.9	1.377	0.229
Error	125	820.1		
(c) *D. antarctica* (Drift and control to day 62)				
Days	7	2962.2	9.648	**0.004**
Treatment	1	207.4	0.524	0.476
Day x Treatment	7	307.0	0.532	0.808
Error	101	576.8		
(d) *D. antarctica* (All treatments to day 7)				
Days	3	2144.3	1.542	0.297
Treatment	2	23227.7	16.907	**0.003**
Day x Treatment	6	1397.1	2.746	**0.016**
Error	118	508.8		
(e) *C. torulosa* (Drift and control to day 43)				
Day	8	1535.98	1.741	0.225
Treatment	1	121.20	0.148	0.704
Day x Treatment	8	881.87	1.292	0.252
Error	144	682.26		
(f) *C. torulosa* (All treatments to day 7)				
Day	3	2390.1	1.349	0.343
Treatment	2	921.1	0.534	0.610
Day x Treatment	6	1786.8	2.269	**0.040**
Error	138	787.2		

Species composition, abundance, and reproductive status of drift

A total of 99 pieces of drift-algae were found in transects around Kaikoura and Banks Peninsula. The drifting algae consisted of 10 species, 9 of which were found in Kaikoura Peninsula transects, and 6 in Banks Peninsula transects (Fig. 2.5a). Transects done at Kaikoura and Banks Peninsula contained *H. banksii* and *D. antarctica*, but *C. torulosa* was absent from all transects. No drifting algae were found in one transect at Kaikoura, and two transects at Banks Peninsula. There was a significant difference in the abundance of algae (average number of plants or plant fragments within transects) between locations ($F_{1,72} = 5.05$, $p<0.05$; Table 2.4a), with more than twice as much drifting algae collected from transects at Kaikoura (68 pieces) than at Banks Peninsula (31 pieces). However, the effect of location on drift abundance depended on species (interaction effect, $F_{8,72} = 2.4$, $p<0.05$), as greater abundances of *Hormosira banksii* and *Marginariella boryana* were found at Kaikoura, and *Macrocystis pyrifera* was more abundant at Banks Peninsula (Tukey HSD, $p<0.01$).

Despite differences in abundance and species composition, there was no significant difference in the average biomass of drift algae per transect between Kaikoura and Banks Peninsula ($F_{1,8} = 0.68$, $p = 0.432$; Table 2.4b). An average of 1892g ± 679.6 ($\bar{x}$ ± s.e) of algae was found at Kaikoura and 1047.2g ± 764.4 ($\bar{x}$ ± s.e) at Banks Peninsula (Fig. 2.5b). However, the effect of location on biomass depended on species (interaction effect, $F_{8,8} = 4.6$, $p<0.05$), as greater biomass of *Marginariella boryana* was found at Kaikoura, and *Macrocystis pyrifera* at Banks Peninsula (Tukey HSD, $p<0.01$).

All drifting algae that were in their reproductive season at the time of sampling and that had retained their reproductive structures, appeared to be reproductive. All *H. banksii*, *D. antarctica* and *Marginariella* collected were reproductively active (Fig. 2.5c). In contrast, only 21% of drifting *Macrocystis* had reproductive blades, as most had only vegetative blades with no holdfasts and associated reproductive structures. All samples with sporophylls also contained holdfasts, indicating that entire plants had to detach from the substratum for reproduction to occur during or following drifting. Beach-cast *D. antarctica* encrusted in barnacles (*Lepas anatifera*) appeared to be reproductively active. The average scutum size was 12mm (range 10-13mm). The scutum of this species grows at a rate of 0.1mmd^{-1} (Green *et al.* 1994). Although growth rates depend on water temperature (Thiel and Gutow 2005b), this barnacle size indicates that plants had been adrift for a minimum of ~120 days.

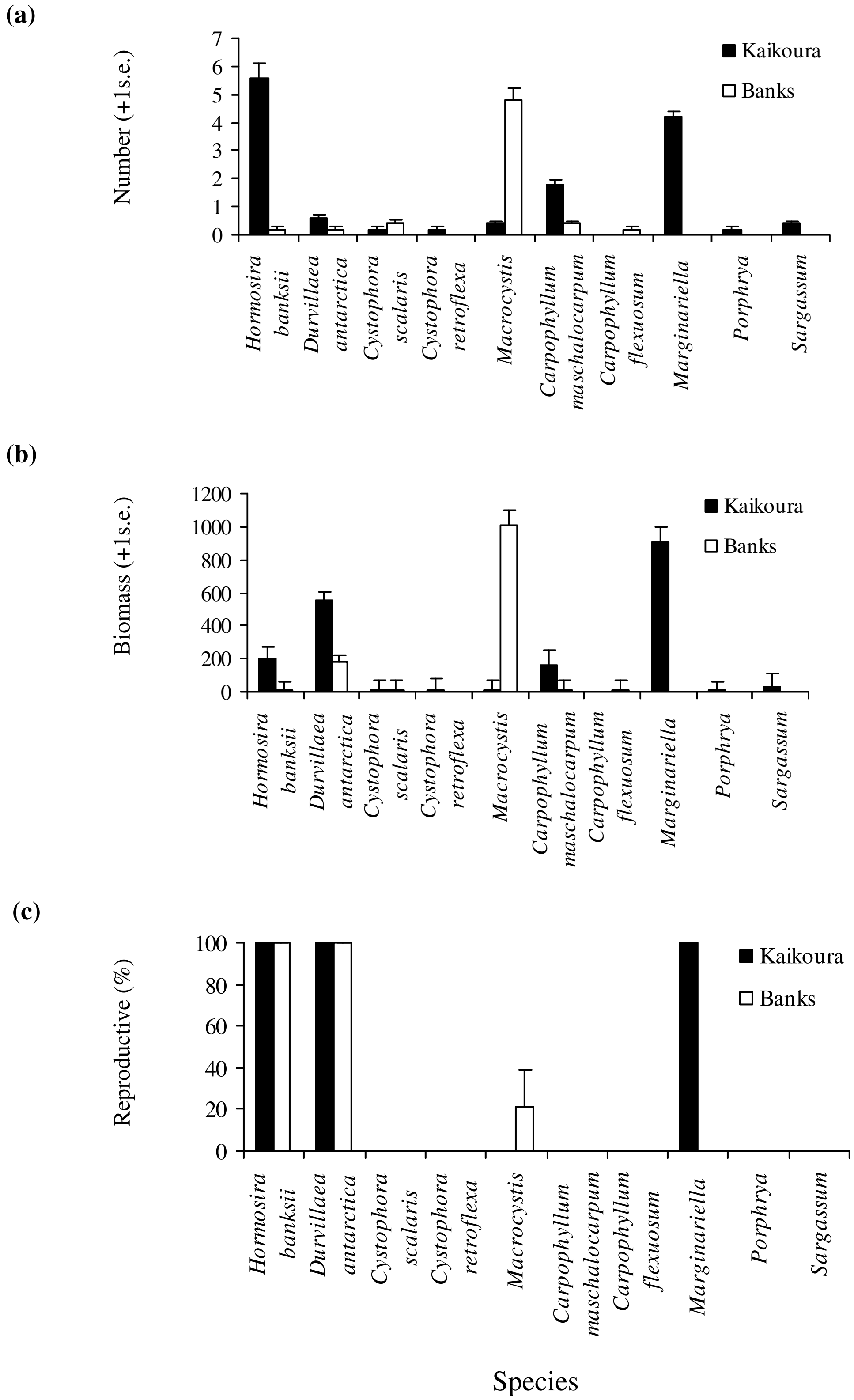


Figure 2.5: The average abundance of each algal species (a), the average biomass (grams) (b) and the reproductive status (percentage reproductive) (c) of drifting algae (whole plants or fronds) found in 5 2km x 10km transects around Kaikoura and Banks Peninsula.

Table 2.4: Two-way ANOVA on the effect of location (Kaikoura and Banks Peninsula) and species on the average number of drifting algae found within transects (a) Two-way ANOVA on the effect of location (Kaikoura and Banks Peninsula) and species on the average wet weight (biomass) of algae found within transects (b).

(a)

Effect	df	MS	F	p
Species	8	9.336	1.01	0.440
Location	1	46.944	5.05	**0.028**
Species x Location	8	22.319	2.40	**0.023**
Error	72	9.294		

(b)

Effect	df	MS	F	p
Species	8	89032	0.034	0.253
Location	1	178734	0.683	0.432
Species x Location	8	12030154	4.60	**0.021**
Error	8	2615251		

2.4 Discussion

Reproductive longevity and viability of drifting and beach-cast algae

Drifting algae

The reproductive viability of detached algae was not significantly reduced over time while drifting, and the reproductive activity of drifting plants did not differ from that of attached onshore populations. Drifting algae continued to release propagules for the duration of the experiments (*H. banksii* 57 days, *D. antarctica* 62 days, and *C. torulosa* 43 days). Additionally, drifting algae continued to release propagules that were viable for as long as they were reproductively active. These results suggest that detached fucoid algae can continue to release viable propagules for weeks or months while adrift, which has important implications for the dispersal potential of these species and their subsequent recruitment capabilities.

Although reproductive activity was variable between sampling days for drifting and attached control algae, the reproductive viability of drifting algae was maintained at high levels as long as sampling material was present. Despite the consistent reduction of drift material throughout the experiments, due to frequent sampling, damage by wave action, and grazing, the reproductive viability of drifting algae was not significantly reduced. This finding is similar to the results of Hernandez-Carmona *et al.* (2006) who found that despite a reduction in biomass, any drifting reproductive *M. pyrifera* blade containing sorus continued to produce viable zoospores. Furthermore, there was no indication of reproductive senescence in drifting *H. banksii* and *D. antarctica* and experiments only ended when bags were removed from the wharf by the public, damaged by storms, or when drift material was completely depleted by sampling. *Cystophora torulosa*, however, was different from the other species. By day 35, drifting *C. torulosa* had begun to degrade and fragment, and significantly fewer gametes were released from drifting treatments on the last two sampling days (35 and 43) compared to attached controls, which may indicate a decline in reproductive activity.

The reduction in number and viability of propagules released from drifting *C. torulosa* could be attributed to two factors. Firstly, the survival and reproductive longevity of drifting algae depends on several environmental factors, including light (Jokiel 1980), and nutrient levels (Edgar 1987). *H. banksii* and *D. antarctica* are positively buoyant and float within the surface waters, but *C. torulosa* remains lower in the water column, just above the sea floor. Light and nutrients may be reduced in deeper cloudy coastal waters and these conditions may be unfavourable for the longevity of bottom drifting species, such as *C. torulosa*. Secondly, grazing by marine invertebrates has been implicated in the degradation of drifting algae (Vandendriessche *et al.* 2007). *C. torulosa* was colonised by numerous amphipods within days adrift, more so than *H. banksii* and *D. antarctica*, and this could have further reduced reproductive longevity. Despite this, however, *C. torulosa* continued to release propagules for the duration of the experiments (43 days), and although viability was variable between days, the viability of these propagules was not significantly reduced over time. Future studies that examine the reproductive longevity of benthic drift, deep in the water column, would be useful to determine the potential for the long-distance dispersal of benthic drifting algae, away from coastal areas.

Beach-cast algae

A large proportion of drifting algae will eventually be washed to shore, and cast up on nearby or distant coasts, but the ability of drifting algae to reproduce once beach-cast is not known. In this study, beach-cast *H. banksii*, *D. antarctica*, and *C. torulosa* desiccated or began to degrade within 14 days of being tethered high on the shore. Furthermore, *C. torulosa* consistently released significantly fewer gametes when beach-cast, compared to drifting and attached treatments.

The speed at which algae desiccate depends largely on the surface-area-to-volume ratio (the larger the ratio, the faster the water loss). In general, smaller, more branched algae lose water fastest (Thomas 2002). Therefore, the consistently lower reproductive output from beach-cast *C. torulosa* may be due to rapid desiccation, as a result of the evaporation of water from a highly branched thallus. In contrast, the branches of *H. banksii* consist of fluid-filled vesicles, which can prevent desiccation and may extend reproductive longevity when beach-cast (Brown 1987). Despite this, however, no propagules were released from beach-cast algae of any species after 14 days, and because the last sampling day before reproductive senescence was 7 days previously (day 7), the reproductive longevity of beach-cast algae may be closer to one week.

These results suggest that there is only a small window of opportunity available for beach-cast material to be re-suspended and continue to release viable propagules as drift. Although *D. antarctica* and *H. banksii* maintained buoyancy in beach-cast treatments and could potentially have been re-suspended, this would have to occur within a week or two of deposition on the shore. The length of time algae remain on the beach is variable and dependent on the tidal cycle and sea conditions (e.g. wind direction and wave action) (Ochieng and Erftemeijer 1999), and the effect of being beach-cast, and subsequently re-suspended, on the reproductive viability of drifting algae is not known. My results indicate that subsequent re-suspension is unlikely to result in reproductively viable drifting algae after a week. These algae are, therefore, essentially lost to the population. Future studies on the frequency of the re-suspension of beach-cast algae, and the effect of being beach-cast, and subsequently re-suspended, on the reproductive longevity of drifting algae would be a valuable contribution to the study of long-distance dispersal by drifting.

Environmental conditions and the longevity of drifting algae

The survival and reproductive longevity of drifting algae on the sea surface depends on several environmental factors, including temperature (Hobday 2000b), light (Jokiel 1980), nutrient levels (Edgar 1987), and grazing (Vandendriessche *et al.* 2007). Tethering algae in the nearshore environment to simulate drifting may restrict the movement of drift into potentially unfavourable environments. In this study, the reproductive activity of drifting fucoids did not differ significantly from attached controls at nearby coastal sites. However, Mayaca *et al*. (2005) found that in central and southern Chile, the reproductive activity of floating *M. pyrifera* was lower than that of attached algae, suggesting that environmental conditions at the sea surface were not optimal for reproductive activity of drifting sporophytes.

Environmental conditions in the open ocean can differ from those within the nearshore environment, and may be unfavourable for drifter longevity (Macaya *et al.* 2005). Therefore, the reproductive longevity of drifting algae may be constrained to near optimal conditions, close to or within their geographic range, and the potential for long-distance dispersal may be reduced in open ocean conditions (Macaya *et al.* 2005). Furthermore, new water and nutrients flow through the mesh bags used to tether the drifting algae to the wharf, whereas naturally drifting algae move within the same body of water for long periods (Thiel and Gutow 2005a), and the longevity and buoyancy of drifting algae may be compromised without sufficient nutrients (Edgar 1987). However, although drifting algae in these experiments were not exposed to the same conditions as drifting seaweeds in the open ocean, all surface-floating algae (*H. banksii* and *D. antarctica*) that were returned to the water maintained their buoyancy for the duration of experiments, and naturally drifting algae have been estimated to maintain their buoyancy for up to 260 days (Smith 2002).

A high tolerance to changes in environmental conditions, such as temperature and salinity, and resistance to degradation and desiccation (for beach-cast algae), may enhance the dispersal potential of drifting algae, and future studies should examine the reproductive longevity of naturally drifting algae over long distances, with movement into different environmental conditions (e.g. temperatures and nutrient levels).

Species composition, abundance, and reproductive status of drift

In transect surveys done around Kaikoura and Banks Peninsula, the abundance and species composition of drift varied considerably between transects, and between study areas. Drifting algae was more abundant in Kaikoura transects compared to Banks Peninsula transects, and algal abundance between transects separated by less than 2km ranged from no drifting algae, to 25 algal clumps. Drifting algae are, therefore, patchily distributed, even over small scales.

Drifting algae were most abundant in surface slicks. Similar results were found off the east coast of Northland, New Zealand, where drifting algae had accumulated within slicks which moved in the direction of the coast, possibly transporting large amounts of drifting algae onshore (Kingsford and Choat 1986). This may increase the likelihood of drift returning to new and distant locations after offshore transport. Furthermore, the abundance of drift arriving at a new location may have implications for fertilisation and recruitment, by decreasing the distance between plants, and reducing density dependent effects.

Previous studies have shown that the abundance of drifting algae varies spatially and temporally, with abundance estimates ranging from <1 to 12,000 drifting macroalgae km^{-2} (reviewed by Thiel and Gutow 2005a). In my study, estimates of drifting algal abundance were 680 (Kaikoura) and 310 (Banks) drifting plants or plant fragments km^{-2}, and biomass estimates were 93.9 kg km^{-2} (Kaikoura) and 52.3 kg km^{-2} (Banks). Numerical abundance estimates are high compared to estimates for other regions, but are consistent with estimates of abundance in the coastal waters of New Zealand (Kingsford 1992). In contrast, the biomass estimates are lower than most estimates of biomass in other studies. Therefore, in my study, drift algae consisted of mostly small, but abundant, plants and plant fragments. However, both biomass and abundance estimates can be seasonally and temporally variable (Thiel and Gutow 2005a). For example, Kingsford (1992) found that some species were highly predictable in their seasonal occurrence in transects done off the Northeastern coast of New Zealand. *Sargassum sinclairii* were only found in spring and summer (September – March), which is when these species detach from their holdfasts during the later stages of reproduction (Schiel 1985).

The dominant component of drifting algae collected from Kaikoura and Banks Peninsula transects was large brown macroalgae (fucoids and laminarians), and the species composition of drift reflected the intertidal and immediate subtidal algal populations on each peninsula. Transects around the Kaikoura Peninsula were dominated by *H. banksii* and *Marginariella*, whereas the most abundant species in Banks Peninsula transects was *Macrocystis*. Smith (2002) found that *D. antarctica* dominated sightings of drifting kelp in the Southern Ocean, and estimated that over 70 million rafts are afloat at any one time, but did not mention if they were reproductive. In my study *D. antarctica* contributed to a relatively low number of sightings. However, due to its large size, its contribution to biomass was relatively high, and all plants sampled were reproductive. Additional evidence for the reproductive longevity of drifting *Durvillaea antarctica* came from several reproductive plants that were beach-cast and encrusted in barnacles (Lepas spp) at Kaikoura. The average barnacle size (12mm) suggested the plants had been adrift for >120 days.

The amphitropical distribution of *M. pyrifera* has been attributed to the detachment and drift of reproductively active plants. However in this study, although *M. pyrifera* accounted for 77% of the observed drifting algae in Banks Peninsula transects, 81% of all drifting *M. pyrifera* lacked holdfasts, and associated reproductive structures, and often single pneumatocysts were observed drifting with no attached fronds. Similar results were found in the Southern Ocean, where surveys of kelp rafts revealed that no drifting *Macrocystis* possessed a hold fast (Smith 2002). *Macrocystis* fronds can become detached from the upper region of the plant, leaving the holdfast and associated reproductive structures, attached to the substratum. Furthermore, although *Macrocystis* fronds are buoyant due to gas filled vesicles, the fertile blades, which are located at the base of the plant, lack these air filled bladders (Adams 1994). If fertile blades become detached from the buoyant fronds, they will most likely sink to the sea floor. Therefore, the abundance of reproductive *M. pyrifera* may be strongly influenced by the occurrence of storm events, which can uproot entire plants (Dayton *et al.* 1992, Reed *et al.* 2004).

Species that do not have external reproductive structures that can potentially become detached from the buoyant plant are highly likely to be reproductive when drifting, if in reproductive season, because even small portions of plants can produce viable gametes. For example, *H. banksii* branches consist of small, buoyant, fluid-filled bladders, or nodes, and gametes are produced in conceptacles located near the surface of all nodes (Adams 1994). The entire blade of *D. antarctica* is buoyant due to gas-filled cells, and gametes are released from conceptacles located over the blade surface (Adams 1994). Therefore, even though these species were less abundant than *M. pyrifera* in some transects, all *H. banksii* and *D. antarctica* plants and plant fragments were reproductive.

Buoyancy of reproductive fronds is an important characteristic of drifting algae and, in this study, *Cystophora torulosa* did not float in the surface waters. This species may disperse by drifting as benthic drift lower in the water column, or when entangled in rafting species on the sea surface. Despite this, *C. torulosa*, was not found in any transects, although other *Cystophora* species (*C. scalaris* and *C. retroflexa*) were found in low abundance.

Summary

The results of this study indicate that drifting algae can continue to release viable propagules for weeks or months following detachment. Intertidal fucoid algae are regularly exposed to increased levels of heat, light and desiccation (at low tide) and are not normally continually immersed. These environmental factors are known to influence reproduction and gamete release and, therefore, it was perhaps surprising that these species remained reproductively viable for so long while adrift.

Drifting algae could travel considerable distances in a few weeks, and release viable gametes at distant sites. However, actual connectivity will depend on several factors, including the ability of drifting algae to move offshore after detachment (chapter 3), and successful fertilisation at new location (chapter 4). Most algae may not be transported long distances offshore, and can be cast up on rocky or sandy beaches within days. Once beach-cast, there appears to be a very small window of opportunity for drift to be re-suspended and transported as reproductively viable drifting plants.

Chapter 3 - Nearshore Dispersal Potential of Drifting Fucoid Algae

3.1 Introduction

The relative success of drifting as a long-distance dispersal mechanism depends on the ability of drift algae to move offshore after detachment. Algae that detach from the substratum may travel considerable distances due to tidal and wind-induced movement of surface waters, if they do not wash immediately to shore (Thiel and Gutow 2005a). Before drifting algae can become entrained in large-scale offshore current systems, however, they must 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, nearshore bathymetry, and waves (Ochieng and Erftemeijer 1999). However, the conditions favourable for movement of drifting algae offshore, and the frequency of offshore dispersal events, are not known.

Recent studies have tracked the movement of naturally occurring and artificially created drifters (Harrold and Lisin 1989, Hobday 2000a, Hernandez-Carmona *et al.* 2006), but none of these drifters originated from the shore. Harrold & Lisin (1989) found that *Macrocystis pyrifera* rafts in Monterey Bay were transported according to prevailing winds, which determined the movement of the surface waters, but release points were 0.2 to 4.6km away from the coast (Harrold and Lisin 1989). In the Southern California Bight, the trajectories of satellite-tracked drifters followed large-scale circulation patterns, which were stronger than wind-influenced surface flow, but drifters were deployed at an average distance of 12.3km from the nearest land (Hobday 2000a). Hobday (2000a) defined a ‘successful connection event’ between populations to be drifters that were deployed less then 10km from the coast, and ended up less then 5km from the coast. Under this definition, 45% of drifters were successful in connecting populations (Hobday 2000a). However, no drifters originated from the shore, so these data are only representative of drift material that had managed to get some distance offshore following detachment (Hobday 2000a) and, therefore, may not represent effective culmination of dispersal in getting back to appropriate inshore habitats.

Dispersal by marine algae is a complex process influenced by a variety of physical and biological factors, including the characteristics of the adult plant and interactions with the nearshore water mass (Gaylord *et al.* 2002). Despite this, the initial export phase of drifting has not been linked to nearshore processes, and the relative ability of drift algae to move into the offshore environment following detachment is largely unknown. Understanding this phase of dispersal, its dependence on nearshore processes, and the relative influence of species characteristics, has important implications for patterns of seaweed recruitment in hydrodynamically complex environments (Gaylord *et al.* 2002). The extent of dispersal may depend on where the plants originated from, and certain times of the year may be more favourable for retention or for dispersal offshore (Paris *et al.* 2007). Furthermore, the relative ability of drifting algae to move offshore after detachment may vary between species.

This chapter investigates the influence of nearshore processes on the initial phase of dispersal, immediately after the detachment of an adult plant from the shore. I specifically test what conditions are favourable for the dispersal or retention of drifting algae, with particular reference to the relative importance of wind versus tidal currents, and if this varies between species.

3.2 Methodology

Because drifting algae are difficult to track and relocate accurately, there are obvious logistical problems when attempting to determine their movement after detachment from the substratum. An alternative is to mimic natural drifting conditions to give some approximation of drifting potential (Hernandez-Carmona *et al.* 2006). Drifting buoys or 'drifters' have often been used to resolve coastal surface currents, and to provide estimates of the dispersal distance and direction of floating drift material (Hobday 2000a). However, the position of an artificial drifter in the water column may prevent accurate determination of actual drift time and influence the direction of drift. Drifting algae float within the surface waters, whereas GPS drifters protrude slightly above the surface of the water, and extend lower in the water column. Therefore, I used tagged drifting algal clumps to compare drift potential between species and to determine if the GPS-tracked drifters accurately mimic the dispersal tracks of drifting seaweed.

The movements of tagged drifting algae and GPS-tracked drifters were determined on ten occasions in March and April 2008 in the nearshore waters of Wairepo Reef, Kaikoura. Drift sets were deployed at the onset of six incoming tides and four outgoing tides during onshore (northeasterly) and offshore (southwesterly) winds (Table 3.1) of varying strength.

The duration of deployments was approximately 4 hours. Tide tables for standard ports were obtained from Land Information New Zealand (LINZ), and wind speed and direction data were obtained from the Kaikoura weather station, courtesy of the National Institute of Water and Atmospheric Research (NIWA), New Zealand, climbase.

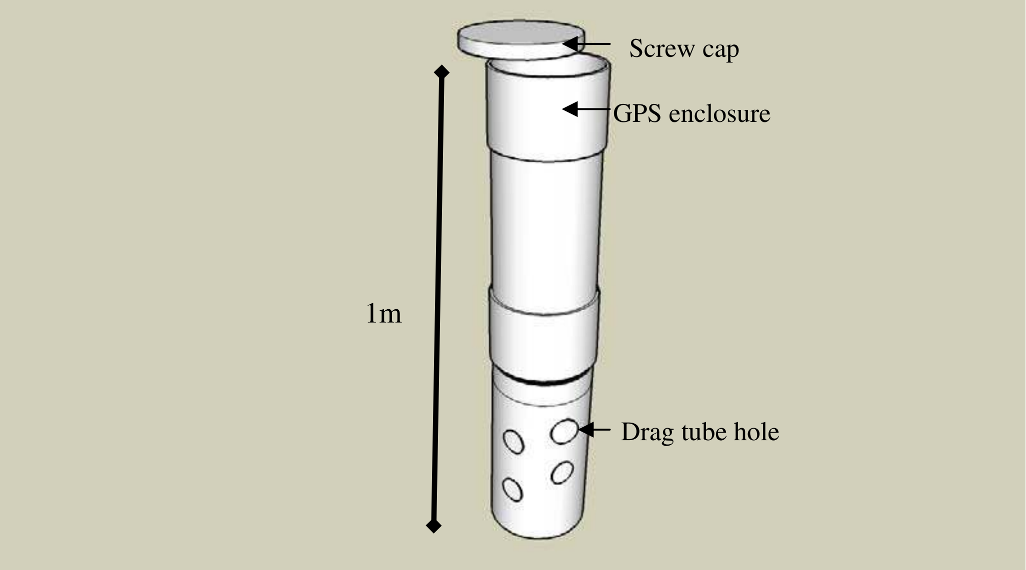
Table 3.1: List of experiments and conditions (tidal direction and wind direction) during deployments of tagged algae and GPS-tracked drifters in March and April 2008.

Experiment number	Deployment date	Tide direction	Wind direction
1	19.3.08	Incoming	Onshore
2	21.3.08	Incoming	Onshore
3	22.3.08	Outgoing	Offshore
4	22.3.08	Incoming	Offshore
5	3.4.08	Incoming	Onshore
6	4.4.08	Incoming	Onshore
7	16.4.08	Incoming	Offshore
8	16.4.08	Outgoing	Onshore
9	17.4.08	Outgoing	Onshore
10	18.4.08	Outgoing	Offshore

Bundles of tagged drifting algae were made by removing *Hormosira banksii*, *Durvillaea antarctica* and *Cystophora torulosa* from the substratum and tagging plants with fluorescent flagging tape. GPS-tracked drifters consisted of a hand-held Garmin Etrex™ Global Positioning System (GPS) housed in a submerged, 1m long (10cm diameter) vertical tubular PVC body (Fig. 3.1). GPS-tracked drifter positions were accurate to within c.5 meters.

For each experiment, there were nine tagged algal drifters for each of the three study species (*H. banksii*, *D. antarctica*, and *C. torulosa*) (i.e., 27 tagged algal clumps in total), and nine GPS-tracked drifters. On each experiment date, a drift set, consisting of one tagged bundle of each algal species, and one GPS-tracked drifter, was placed at three shore heights (high, mid, and low shore) on Wairepo Reef (Fig. 3.2). There were three replicate drift sets within each. The release locations were labelled 1 to 9, and the flagging tape on the algal clumps and the body of the GPS-tracked drifters within each drift set were labelled with their release location.

(a)



(b)

Figure 3.1: Diagram of a GPS-tracked drifter constructed from 10cm diameter PVC tubing (a) and a photograph of GPS-tracked drifters drifting during a deployment in the nearshore waters of Wairepo Reef, Kaikoura (b).

Drift sets were deployed at low tide (prior to an incoming tide), or at high tide before the tide began to recede. At the beginning of each experiment, the original position of release of each drift set was marked using a hand-held GPS, and the GPS units in the GPS-tracked drifters were turned on to track their paths from the release location. The locations of the tagged drifting algae were marked using hand-held GPS throughout the tidal cycle from a boat, to track their movement, and to calculate velocities and overall displacement. If a GPS-tracked drifter was cast up on the beach, or when removed from the water at the end of the experiment, the GPS was turned off immediately. On completion of the tidal cycle the location of all beach-cast and drifting tagged algae was marked again using hand-held GPS, and the species and their initial release locations were recorded.

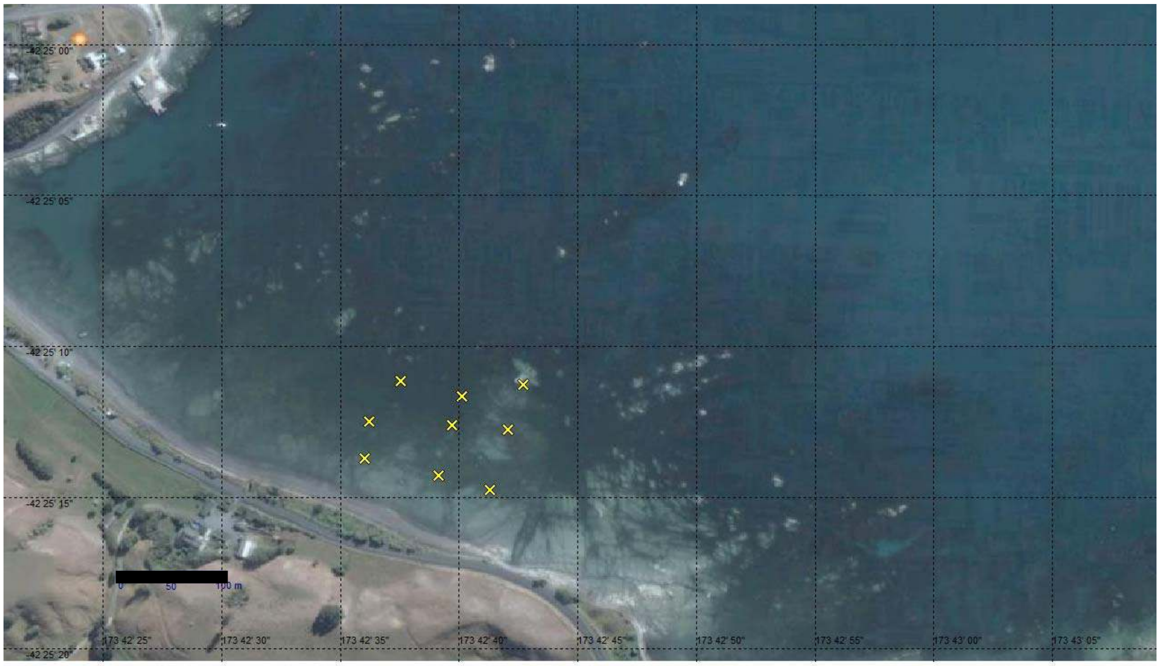


Figure 3.2: The release locations of ‘drift sets’ (one tagged algal clump of each species, and one GPS-tracked drifter) at three different shore heights (high, mid, and low) on Wairepo Reef, Kaikoura. The scale bar is 100m.

3.3 Results

The GPS-tracked drifters moved in the same direction as surface drifting *H. banksii* and *D. antarctica* in all experiments (Fig. 3.3). In contrast, *C. torulosa* sat lower in the water column, and moved in different directions to *H. banksii*, *D. antarctica* and GPS drifters. The prevailing wind directions during these experiments were primarily either northeasterly (onshore) or southwesterly (offshore) in direction (Fig. 3.4). Tagged algae and GPS-tracked drifters deployed during onshore (northeasterly) winds and incoming tides, generally moved onshore (Fig. 3.5a), and most were beach-cast within one tidal cycle. Tagged algae and GPS-tracked drifters deployed during offshore (southerly) winds and outgoing tides, generally moved offshore (Fig. 3.5b).

GPS-tracked drifters and tagged algae deployed during offshore (southwesterly) winds and incoming tides generally moved offshore, although an influence of tidal direction was evident. The influence of tidal direction may occasionally result in drift being transported alongshore (Fig. 3.6a). GPS-tracked drifters and tagged algae deployed during onshore (northerly) winds and outgoing tides generally moved onshore, and were either pushed on to the shore by onshore wind-induced currents, or dropped on the reef as the tide receded (Fig. 3.6b).

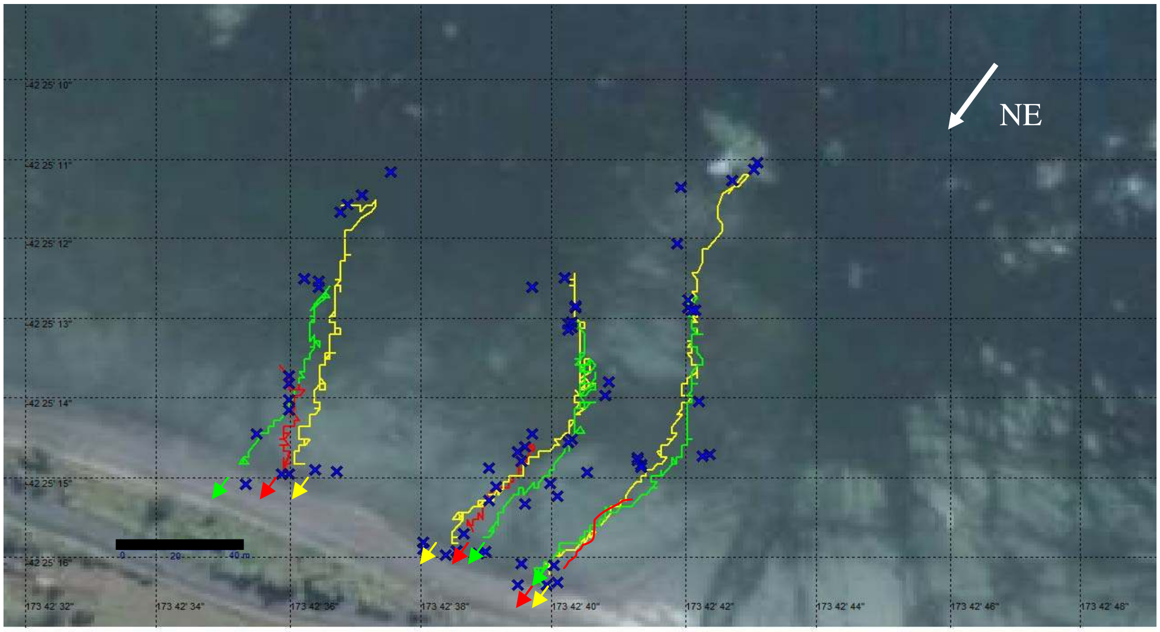
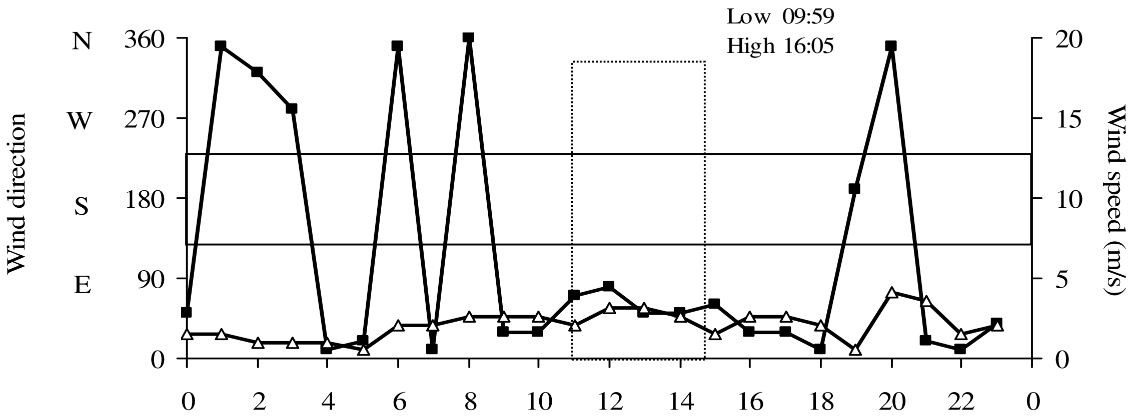
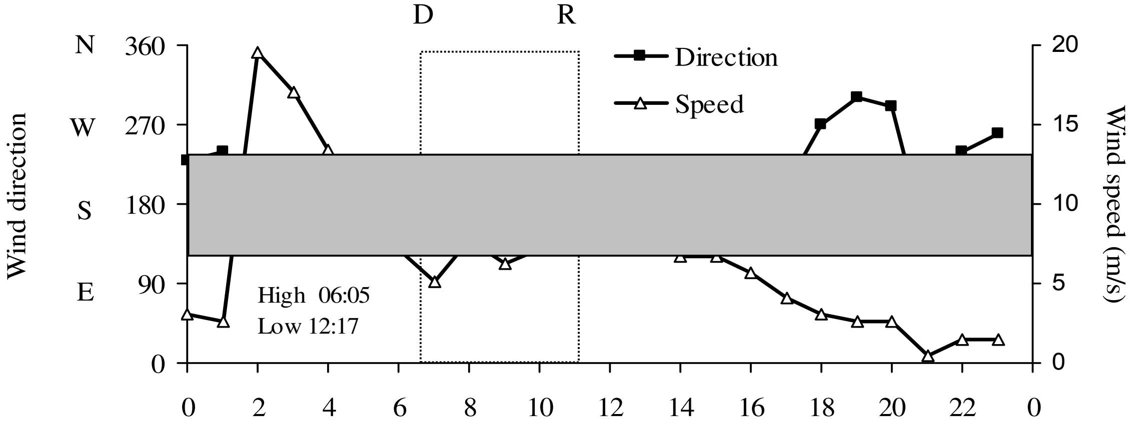


Figure 3.3: An example of the movement of surface drifting tagged algae (*H. banksii* and *D. antarctica*) (blue crosses) and GPS-tracked drifters (coloured lines) in an experiment done during an incoming tide and onshore wind deployment on the 4th April 2008. Drift sets were released from low (yellow lines), mid (green lines) and high (red lines) shore. Arrows indicate drift direction. Drifters were deployed for approximately 4 hours. The scale bar is 50m. White arrow shows prevailing northeasterly (NE) wind direction.

(a) Onshore wind, incoming tide (see Fig. 3.5a)



(b) Offshore wind, outgoing tide (see Fig. 3.5b)



(c) Offshore wind, incoming tide (see Fig. 3.6a) and onshore wind, outgoing tide (see Fig. 3.6b)

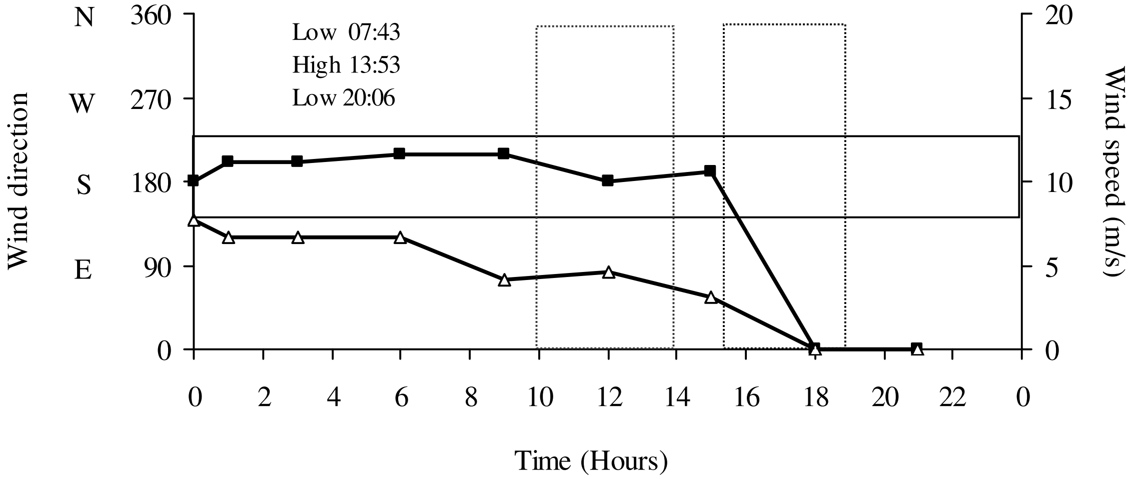
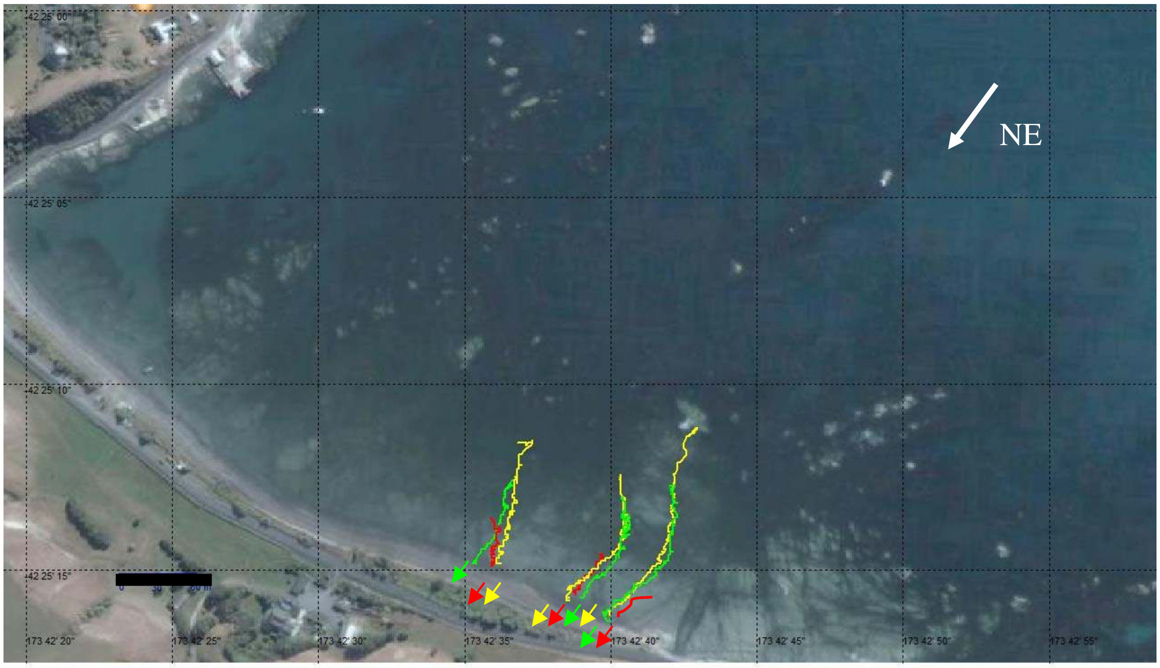


Figure 3.4: Wind direction and speed data for four drifter releases during an onshore wind and incoming tide deployment on the 4th April 2008 (a), an offshore wind and outgoing tide deployment on the 22nd March 2008 (b) and an offshore wind and incoming tide, and onshore wind and outgoing tide deployment on the 16th April 2008. Shaded bar indicates offshore winds and dotted vertical bars indicate drifter deployment (D) to re-capture (R).

(a) Incoming tide and onshore wind



(b) Outgoing tide and offshore wind

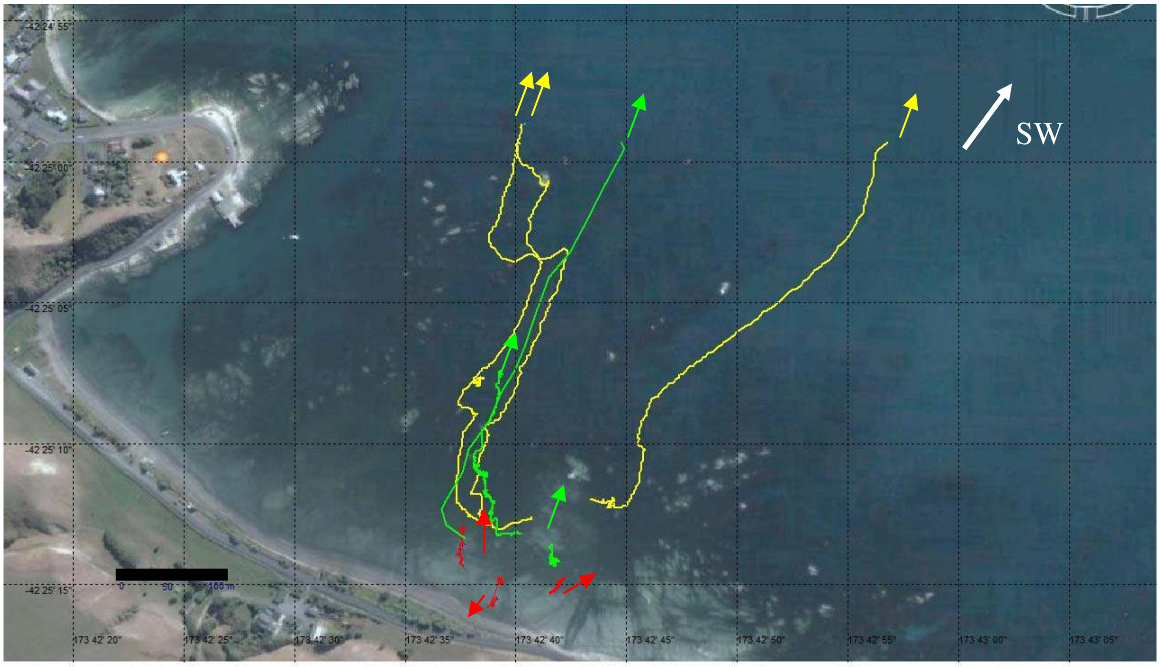
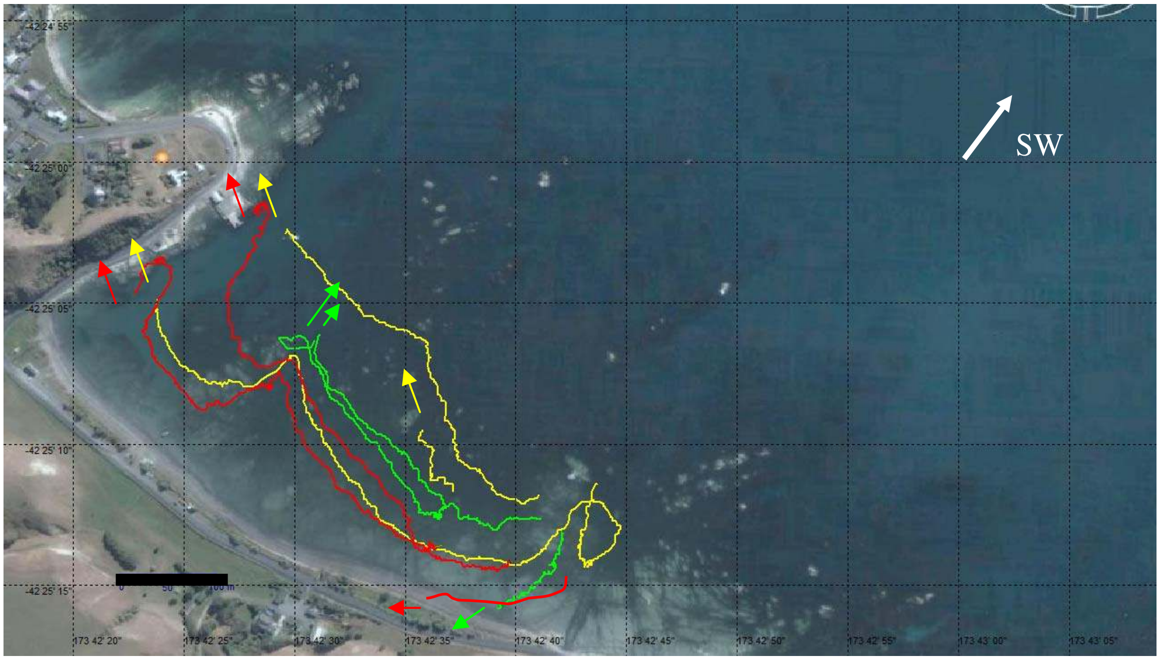


Figure 3.5: The movement of GPS-tracked drifters (coloured lines) during an incoming tide and onshore (northeasterly) wind deployment on the 4th April 2008 (scale bar 50m) (a) and an outgoing tide and an offshore (southwesterly) wind deployment on the 22nd of March 2008 (scale bar 100m) (b). Drift sets were released from low (yellow lines), mid (green lines) and high (red lines) shore. Arrows indicate drift direction. Drifters were deployed for c. 4 hours. White arrow shows prevailing wind directions (NE = northeasterly, SW = southwesterly).

(a) Incoming tide and offshore wind



(b) Outgoing tide and onshore wind

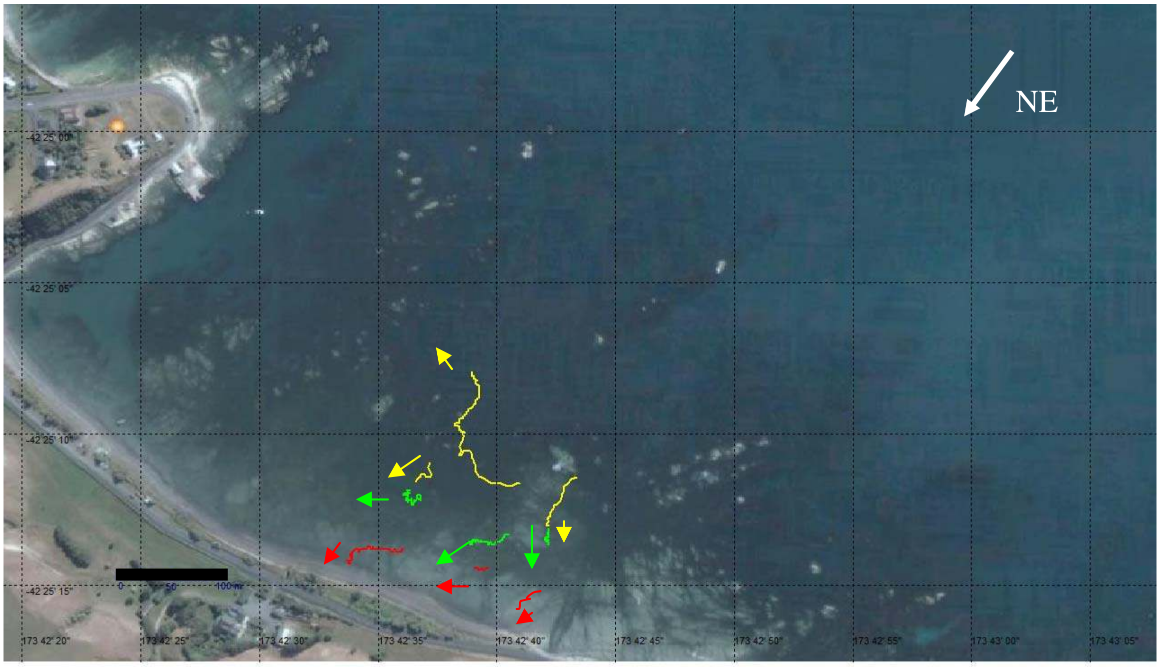
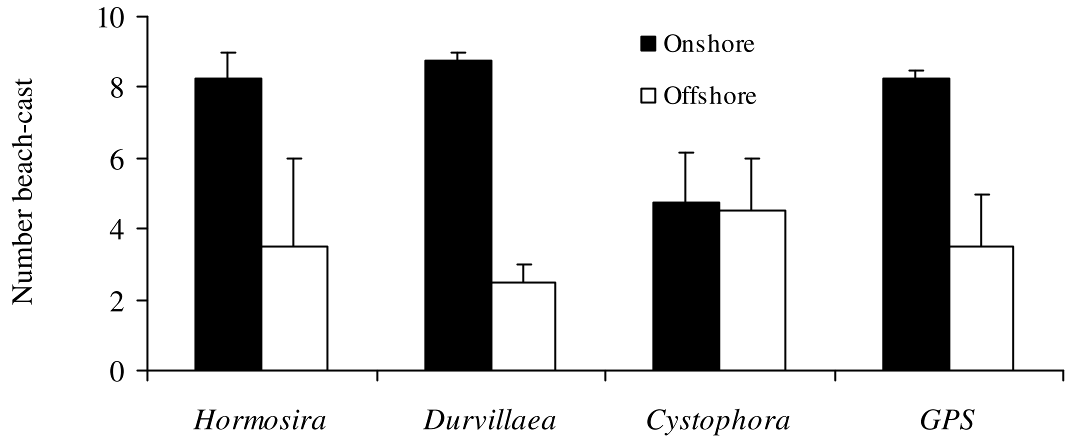


Figure 3.6: The movement of GPS-tracked drifters (coloured lines) during an incoming tide and offshore (southwesterly) wind (a), and an outgoing tide and onshore (northerly) wind (b) on the 16th of April 2008. Drift sets were released from low (yellow lines), mid (green lines) and high (red lines) shore. Arrows indicate drift direction. Drifters were deployed for c. 4 hours. The scale bar is 100m. White arrow shows prevailing wind direction (NE = northeasterly, SW = southwesterly).

To test whether wind direction, tidal direction and height of release on the shore affected the number of tagged algae and GPS-tracked drifters that were beach-cast after one tidal cycle, a four-way ANOVA was done comparing wind direction (onshore and offshore), tides (incoming and outgoing), shore height of release (low, mid and high), and drifter type (*Hormosira banksii*, *Durvillaea antarctica*, *Cystophora torulosa* and GPS-tracked drifters) (Table 3.2).

The release height on the shore did not affect the number of tagged algae and GPS drifters that were beach-cast after on tidal cycle, regardless of wind and tidal direction ($F_{2,54}$ = 0.808, p = 0.452). Therefore, because p>0.25, shore heights were combined (Fig 3.7). Wind direction had a significant affect on the number of tagged algae and GPS-tracked drifters that were beach-cast after one tidal cycle ($F_{1,54}$ = 92.297, p<0.001). Offshore winds were most favourable for dispersal offshore (Tukey HSD, p<0.001), regardless of tidal direction. However, the influence of prevailing wind direction varied by drifter type (wind x drifter interaction, $F_{3,54}$ = 12.01, p<0.01). This was due to a significant difference in the number of *C. torulosa* beach-cast after one tide compared to all other drifter types (*H. banksii*, *D. antarctica* and GPS-tracked drifters), regardless of wind direction. Approximately 90 to 100% of *H. banksii*, *D. antarctica* and GPS-tracked drifters were beach-cast after one tide in experiments done during onshore winds, and 20 – 30% were beach-cast in experiments done during offshore winds. In contrast around 50% of *C. torulosa* were beach-cast after one tidal cycle, regardless of winds direction. Therefore, wind direction significantly influenced the movement of *H. banksii* and *D. antarctica* and GPS-tracked drifters, but not *C. torulosa*.

(a) Incoming tide



(b) Outgoing tide

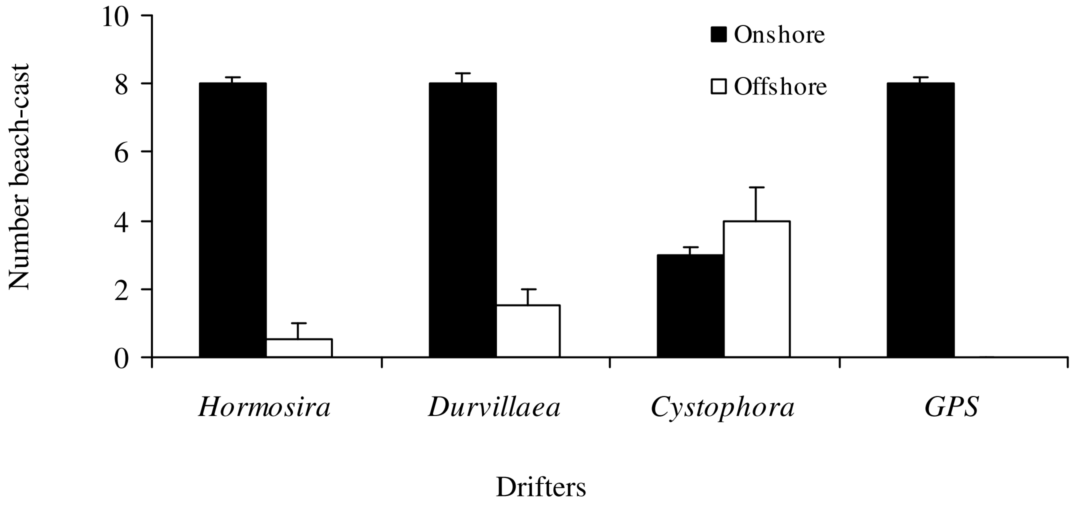


Figure 3.7: The number of tagged algae (*H. banksii, D. antarctica* and *C. torulosa*) and GPS-tracked drifters (GPS) that were beach-cast after one tidal cycle (4 hour deployment) during incoming (a) and outgoing (b) tides and onshore (black bars) and offshore (white bars) winds (+1s.e).

Table 3.2: ANOVA on the effect of wind direction (onshore and offshore), tide at release (incoming and outgoing), drifter type (*H. banksii*, *D. antarctica*, *C. torulosa* and GPS-tracked drifters), and release height on the shore (high, mid and low) on the average number of drifters beach-cast after one tidal cycle.

Effect	**SS**	**df**	**MS**	**F**	**p**
Wind	62.813	1	62.813	92.297	**0.000**
Tide	1.191	1	1.191	1.751	0.191
Drifter	2.247	3	0.749	1.101	0.357
Shore height	1.099	2	0.549	0.808	0.452
Wind x Tide	1.407	1	1.407	2.068	0.156
Wind x Drifter	24.515	3	8.171	12.001	**0.000**
Tide x Drifter	0.321	3	0.107	0.158	0.924
Wind x Shore height	0.450	2	0.225	0.331	0.720
Tide x Shore height	1.207	2	0.603	0.887	0.418
Drifter x Shore height	2.211	6	0.368	0.542	0.774
Wind x Tide x Drifter	2.190	3	0.730	1.073	0.368
Wind x Tide x Shore height	0.126	2	0.063	0.093	0.912
Wind x Drifter s x Shore height	1.778	6	0.296	0.436	0.852
Tide x Drifter x Shore height	2.570	6	0.428	0.630	0.706
Wind x Tide x Drifter x Shore ht.	0.827	6	0.137	0.203	0.975
Error	36.75	54	0.680		

The average velocities (m hr^{-1}) of movement throughout the drifting period were calculated for tagged algae and GPS-tracked drifters over all experiments. Velocities for tagged algae were obtained by following algae for one minute after release and calculating velocity by the distance travelled during this time. In contrast, the GPS units tracking the movement of GPS-tracked drifters recorded the velocities of GPS drifters over the entire release period. Although GPS-tracked drifters moved in the same direction as the surface drifting tagged algae, both *C. torulosa* and GPS-tracked drifters travelled slower (*C. torulosa*, 380 m hr^{-1}, GPS drifter, 234.83 m hr^{1}) than *H. banksii* (785 m hr^{-1}) and *D. antarctica* (823 m hr^{-1}) across all experiments (Fig. 3.8). This difference was largely due to *C. torulosa* rolling along the bottom instead of floating in the surface waters, and the drag created by the drift tube of the GPS-tracked drifters.

Although velocities are important to determine the speed at which drifting algae can potentially travel, overall displacement is of primary interest to determine actual dispersal potential. Consequently, the overall displacement of drifters (*H. banksii*. *D. antarctica*, *C. torulosa*, and GPS-tracked drifters) in one tidal cycle (4 hour deployment) was calculated. The effect of release location (high, mid and low) and drifter type, on overall displacement during onshore and offshore winds was tested using two-way ANOVA (Table 3.3).

During onshore winds, the displacement of both algal and GPS drifters released at different shore heights differed significantly ($F_{2.129} = 18.88$, $p<0.001$) (Table 3.3a). This is because most drifters moved onshore during onshore winds, and were beach-cast after one tidal cycle. Therefore, the displacement distance of all drifters was generally the distance between the release location and the shore. For example, drifters released from the low shore were displaced c. 360m before being beach-cast, while those released from the mid shore and high-shore drifters were displaced c. 300m and c. 200m respectively (Fig. 3.9).

During offshore winds, the linear displacement distance of drifters was also significantly affected by the release height on the shore and drifter type (Table 3.3b). Drifters released on the high shore generally travelled shorter distances in one tide because they were usually found dragging over the reef or trapped in crevices for long periods. The displacement difference between species was due to significantly lower displacement of *C. torulosa*, which travelled c. 300m during offshore winds, whereas *H. banksii*, *D. antarctica* and GPS drifters travelled between 600 and 900m in an offshore direction, under the same conditions.

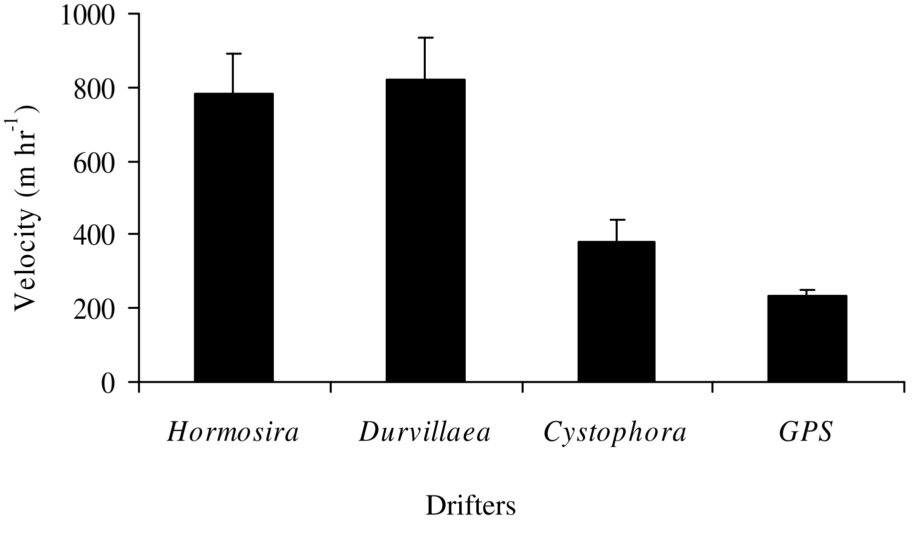
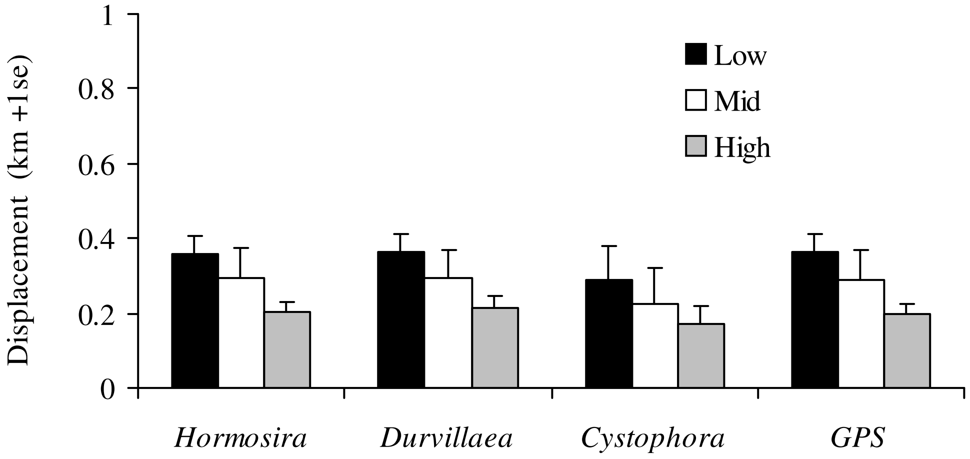


Figure 3.8: Average velocity (m hr^{-1}), for tagged algae (*H. banksii*, *D. antarctica*, *C. torulosa*) and GPS-tracked drifters (+1s.e).

(a) Onshore



(b) Offshore

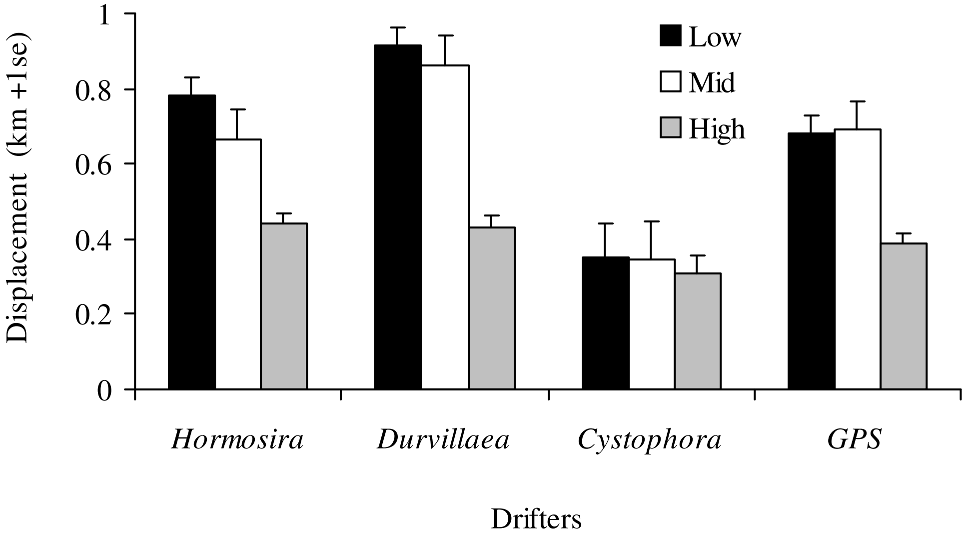


Figure 3.9: The average linear displacement of drifters (*H. banksii*, *D. antarctica*, *C. torulosa* and GPS-tracked drifters) in one tide (4 hour deployment) (+1s.e.), released from the low, mid and high shore during onshore (a) and offshore (b) wind.

Table 3.3: ANOVA on the effect of release height on the shore (low, mid and high), and drifter type (*H. banksii*, *D. antarctica*, *C. torulosa*, and GPS-tracked drifters), on the overall displacement (linear distance travelled) of drifters deployed during onshore (a) and offshore (b) winds.

(a) Onshore winds

Effect	**df**	**MS**	**F**	**p**
Shore height	2	0.250	18.889	**0.000**
Drifters	3	0.030	2.327	0.077
Shore height x Drifters	6	0.001	0.088	0.997
Error	129	0.013		

(b) Offshore winds

Effect	**df**	**MS**	**F**	**p**
Shore height	2	0.622	10.008	**0.000**
Drifters	3	0.724	11.646	**0.000**
Shore height x Drifters	6	0.043	0.693	0.655
Error	94	0.062		

3.4 Discussion

The movement of drifting algae offshore, to the point where long-distance dispersal may be possible, appears to occur periodically, and under specific environmental conditions. In all experiments, the dominant factor influencing the movement of drifters was wind direction, rather than tidal movement or the position of release in the tidal zone. However, some influence of tidal direction was detected, and the relative influence of wind direction on the movement of drifting algae varied between species.

Surface drifting tagged algae (*H. banksii* and *D. antarctica*) and GPS drifters generally followed the direction of the prevailing winds, which were predominantly northeasterly (onshore) or southwesterly (offshore). *H. banksii*, *D. antarctica* and GPS-tracked drifters deployed during northeasterly winds generally moved onshore (southwest), and most were beach–cast within one tidal cycle. Prevailing southwesterly winds moved the surface drifting algae and GPS-tracked drifters to the north-east, in an offshore direction. However, some tidal influence was also detected in drifter tracks, and this appeared to be of increased importance during periods of decreased wind strength. Onshore winds and outgoing tides deposited most surface drifting algae and GPS drifters onto the reef as the tide receded. Shorter, localised dispersal of this nature will result in greater chances of mixing populations within bays. The greatest potential for offshore transport, and the possibility of subsequent long-distance dispersal, was during periods when prevailing offshore winds and outgoing tides coincided.

In contrast, wind direction and tidal direction did not significantly influence the amount of *C. torulosa* that was beach-cast after one tidal cycle. The differences between species were largely due to the position of the drifting algae in the water column. Drifting algae can be exported to nearby or distant sites either as benthic drift suspended near the sea floor (Harrold & Reed 1985, Holmquist 1994; Belsher & Meinesz 1995; Brooks & Bell 2001) or as floating algae in the surface waters. In my study, *D. antarctica* and *H. banksii* were found to float within the surface waters, whereas *C. torulosa* sat lower in the water column and tended to roll along the sea floor. Algae near the bottom may become entrained in currents moving at different velocities and directions than those within the surface waters, due to vertical shear in the water column, and this is likely to influence their dispersal potential. In all experiments, *C. torulosa* generally moved shorter distances and at slower velocities, compared to surface-drifting species (*H. banksii* and *D. antarctica*) due to entanglement in the cracks and crevices of the substratum. Despite this, *C. torulosa* may still be dispersed by drifting, either as benthic drift, tumbling along the sea bottom, or in the surface waters, when entangled with other surface drifting species, but the most likely probability for this species is short-range dispersal within localised areas. Because of limited buoyancy, this species seems to have less chance of longer range drifting.

Because the upper region of the water column typically moves in the same direction as the wind, surface-floating drift algae and GPS-drifters should behave similarly (Hobday 2000a). Although the GPS drifters used in our study protruded slightly above the surface of the water, and extended lower in the water column (75cm), they accurately moved in the same direction as the surface-drifting seaweed (*D. antarctica* and *H. banksii*). GPS-drifters can, therefore, be used to give a reasonable approximation of the dispersal direction of surface drifting algae. However, because GPS drifters travel considerably slower than algae, they will not give an accurate indication of time a-drift. The average velocity of GPS-tracked drifters was 234m hr^{-1} (5.24km day^{-1}). This is similar to the rates determined in studies that used radio and satellite-tracked drifters to infer the dispersal paths and velocities of drifting algae: 4.92km day^{-1} (Harrold and Lisin 1989), 7.15km day^{-1} (Hernandez-Carmona *et al.* 2006), and 8.5km day^{-1} (Hobday 2000a), but slower than tagged surface drifting algae (*H. banksii* and *D. antarctica*).

These results show that the short-term movement of drift in the nearshore environment is strongly influenced by wind and wind-induced surface currents. Therefore, drifting velocities and displacement distances are likely to be largely determined by the strength of the prevailing wind. *H. banksii* and *D. antarctica* travelled at relatively high speeds and potentially could be transported far enough offshore to reach coastal currents. Offshore winds which coincide with outgoing tides produce the conditions most likely to lead to movement out of coastal bays and into larger oceanic currents. Clearly, there are other factors that will influence drift, including bathymetry, coastal topography and the magnitude and direction of waves. Furthermore, the movement of drifting algae in relation to prevailing winds may not be the general pattern beyond the north-eastern side of the Kaikoura Peninsula. The orientation of the detachment site in relation to wind direction, and differences in the direction of prevailing winds at different locations, will influence the transport of drift. For example, much of the coastline along the South Island of New Zealand is orientated parallel to the prevailing northeasterly and southwesterly winds, and detached algae may be transported longer distances before being beach-cast due to alongshore winds and currents. The complex currents and geography around New Zealand make it difficult to predict the connectivity of algal populations, and longer-term tracking, which was beyond the scope of this study, would help clarify the possibilities of movement into offshore current systems.

Bathymetry

Most algae within coastal current systems are likely to remain near the coast. The potential for truly long-distance dispersal will depend on moving out of coastal inlets and bays. Here, the movement of the drifters was clearly influenced by the nearshore bathymetry and geomorphology of the shoreline. Drifters clearly followed subtidal channels and moved around subtidal obstacles, and were often found trapped in large crevices at low tide. Although further analysis of this was beyond the scope of this study, it is clear that coastal geopmorphology will influence the probability of drifting algae getting trapped in inlets and bays or moving offshore into major current systems.

Ecological consequences

Dispersal may be temporally variable, with certain times of the year more favourable for retention or dispersal (Cowen et al., 2002). Prevailing wind directions are seasonally variable

(Fig. 3.10a), and reproductive periodicity varies considerably among species (Hoffmann 1987, Brawley and Johnson 1992). Periods favourable for dispersal offshore may be unimportant if no reproduction is occurring. Therefore, seasonal differences in the movement of drift following detachment could have significant implications for long-distance dispersal, and successful recruitment at particular times.

Northeasterly (onshore) winds prevail around the Kaikoura Peninsula from late spring to early autumn (November-March), as they do along much of the east coast of the South Island, New Zealand. The movement of GPS-tracked drifters and tagged algae in my study suggest that during periods of prevailing northeasterly winds, detached algae along much of the east coast will be deposited on the shore, or retained very near shore. *H. banksii* and *Cystophora* spp. are reproductive year-round, but pulses in reproductive activity are highly seasonal, with peak settlement associated with reproductive activity occurring in spring and early summer (Schiel 2004). Year-round reproduction may enable *H. banksii* and *C. torulosa* to maximize their reproductive success, by taking advantage of periods when favourable environmental and biological conditions for dispersal offshore coincide. Furthermore, following dispersal offshore, drifting algae must return to the coast to a new and suitable habitat. *H. banksii* and *C. torulosa* may take advantage of onshore winds for their return to the shore following dispersal away from the coast.

In contrast, *D. antarctica* is reproductively active only in the winter months (May-August). Strong southwesterly (offshore) winds associated with winter storms, are common along the east coast of the South Island during autumn, winter and early spring (April-October) (Fig. 3.10a). Offshore winds appear to be most important for the transport of drifting algae away from the coast and, once entrained in larger oceanic currents, could lead to transport over long distances. *D. antarctica* could, therefore, take advantage of the offshore wind-driven currents that occur during these months, and associated storm events that can detach algae from the shore (Dayton *et al.* 1984). Furthermore, in Kaikoura, the average wind strength was greatest in June and October (Fig. 3.10b), which are months associated with prevailing offshore winds. The apparent importance of wind direction coupled with wind strength indicates that these months are particularly favourable for the offshore dispersal of drifting algae.

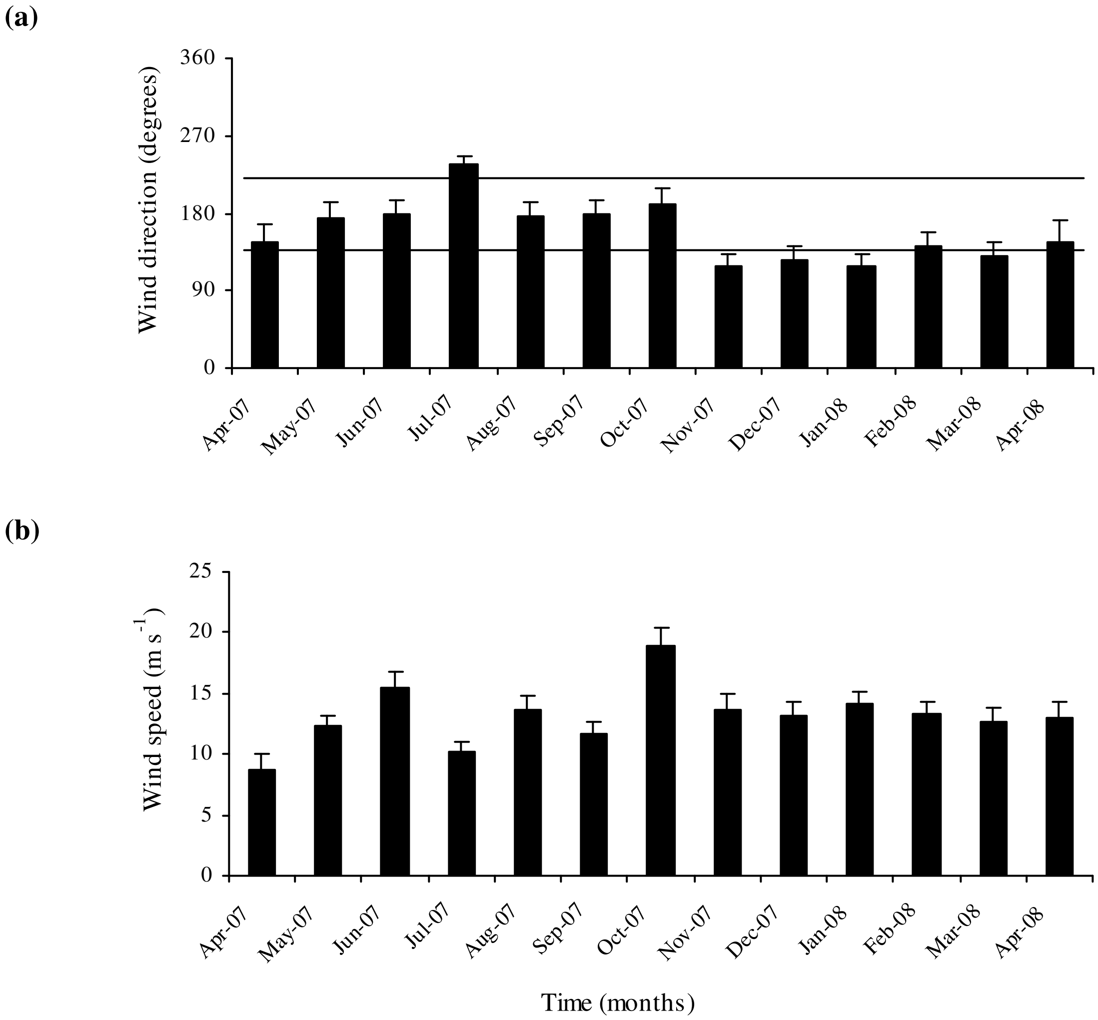


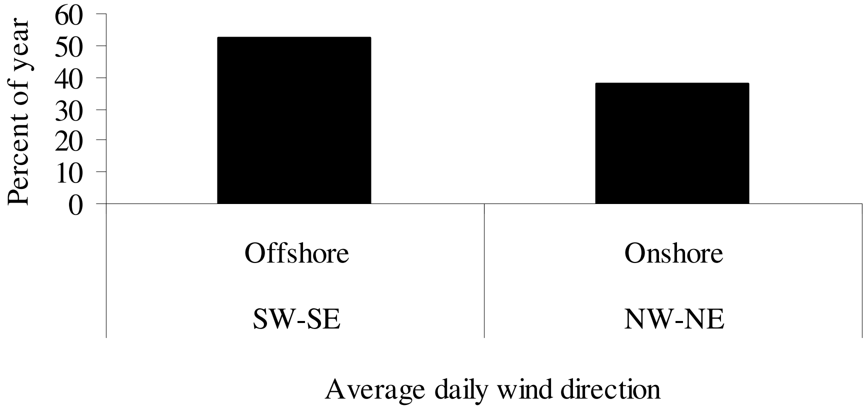
Figure 3.10: Monthly maximum daily wind direction (degrees +1s.e.) (a) and monthly average daily wind speed (m s^{-1} +1s.e.) (b), from April 2007 to April 2008 (Kaikoura weather station daily average data courtesy of NIWA climbase). Area between black lines represents southerly (offshore) winds.

Models of dispersal

Understanding the relative influence of nearshore processes on the movement of drifting algae has significant implications for models and predictions involving dispersal. In New Zealand, tides are semi-diurnal, with two outgoing tides and two incoming tides each day. Therefore, if prevailing winds are offshore in direction, there will be two periods each day that are highly favourable for dispersal offshore. Furthermore, there is the potential to predict not only the seasonal periods that may be most likely for offshore dispersal or retention onshore (see above), but also the frequency of potential dispersal events.

Using wind data from April 2007 and April 2008, we can show that wind direction was favourable for dispersal away from the east coast for 52% of the year, and onshore retention 38% of the year (Fig. 3.11a). Furthermore, the most frequent daily average wind directions were northeasterly (108 days) and southerly (120 days) (Fig. 3.11b), Therefore, given there are two outgoing tides and two incoming tides each day, there were 216 periods highly favourable for the movement of drifting algae toward the coast, where it will most likely be cast up on rocky or sandy beaches, and 240 periods highly favourable for the dispersal of drifting algae offshore. Further studies are required to determine the frequency of long-distance dispersal events away from coastal areas, resulting from the offshore transport of drift in the nearshore environment, to understand the ecological and evolutionary importance of these periods, and how they contribute to population connectivity.

(a)



(b)

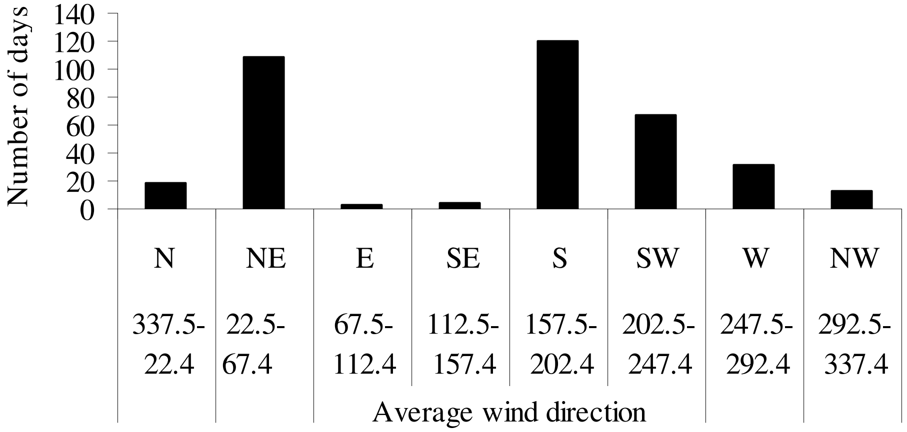


Figure 3.11: Graph showing the percentage of the year (April 2007 to April 2008) the average daily wind direction was offshore (SW-SW; 247.4-112.4 degrees) and onshore (NW-NE; 292.5-67.4 degrees) (a), and daily average wind direction over one year (April 2007 to April 2008) (b) (Kaikoura weather station courtesy of NIWA climbase).

Summary

Based on the direction and velocities of GPS-tracked drifters and tagged algae, the results of this study show that drifting algae can be transported offshore following detachment, and that environmental conditions are sometimes highly favourable for offshore dispersal. Although this area merits further study, the ability of surface drifting algae to move offshore after detachment appears to be predominantly influenced by wind direction. However, the movement of drifting algae is also influenced by the direction of the tide. The relative influence of tidal direction appeared to depend on the strength of the prevailing wind, and, similarly, the relative influence of wind direction will most likely depend on the strength of the tidal currents. Therefore, although offshore winds are favourable for the dispersal of drift away from the shore, periods where prevailing offshore winds and outgoing tides coincide are particularly important for the offshore transport of detached drifting algae within the nearshore environment.

Chapter 4 - External Fertilisation of Fucoid Algae: the Importance of Proximity between Gametes

4.1 Introduction

For drifting to be a successful mechanism of long-distance dispersal, fertilisation and recruitment must occur after arrival at distant sites. Even if drifting algae are transported long distances, and are reproductively viable while adrift, a potentially limiting factor in their effectiveness is the process of fertilisation. This can be exacerbated for dioecious species if male and female plants are separated during the drift.

Dioecious fucoids have direct external fertilisation, with males releasing motile, biflagellated sperm, and females releasing larger, non-motile eggs into the surrounding water column. Subsequent fertilisation depends on successful gamete encounters after release from adults. Therefore, the distance between gametes is crucial, and recruitment will occur only if male and female plants arrive at suitable habitat in close enough proximity for fertilisation to occur. Laminarians, which have an obligate benthic developmental stage before gametogenesis, require male and female gametophytes to be within approximately 1mm of each other for fertilisation and recruitment (Reed 1990). Therefore, monoecious species may be more successful on arrival at new locations, but only if selfing occurs, and without negative consequences for offspring.

Studies of natural gamete release events in fucoid algae have found fertilisation success is close to 100% (Brawley and Johnson 1992, Pearson and Brawley 1996, Serrao *et al.* 1996, Berndt *et al.* 2002). However, natural populations of fucoid algae often form dense stands over large areas (Schiel 2004, Schiel and Foster 2006), which undoubtedly helps maximize egg-sperm interactions. Furthermore, the synchronous release of gametes from large source populations can reduce the effects of gamete dilution and further increase the frequency of gamete encounters (reviewed in Santelices 2002). Although detached algae can form dense piles high on the shore, it can also be widely spaced along the drift line on open coasts and, for dioecious species, there may be considerable distances between plants of the opposite sex. In these cases, before fertilisation can occur, gametes from one individual may have to travel tens to hundreds of centimetres before encountering same-species gametes of the opposite sex, and so reducing the probability of successful fertilisation.

Fertilisation success has been shown to decrease as the distance from potential mates increases in several invertebrate species (Pennington 1985, Denny 1987, Denny and Shibata 1989, Yund 1990, Levitan 1991a, Marshall 2002). Almost all rafting organisms found on drifting substrata have internal fertilisation, as successful external fertilisation is less likely to occur due to low gamete concentrations (Thiel and Gutow 2005b). Factors known to influence fertilisation success include synchrony of gamete release (Pennington 1985, Levitan 1991a, Sewell and Levitan 1992, Marshall 2002), gamete dilution after release (Pennington 1985, Denny and Shibata 1989, Levitan *et al.* 1991, Denny *et al.* 1992, Levitan *et al.* 1992), gamete longevity (Levitan *et al.* 1991, Meidel and Yund 2001, Williams and Bentley 2002), current velocity (Pennington 1985, Yund 1990, Levitan 1991a, Levitan *et al.* 1992) and the density of the source populations (Pennington 1985, Levitan 1991b). These factors also influence the fertilisation success of marine algae (Reed *et al.* 2004, Bobadilla and Santelices 2005, Gaylord *et al.* 2006). However, the effect of distance between gametes is unknown for most species.

Hormosira banksii and *Durvillaea antarctica* are both dioecious species. Therefore, specific parental distances may be crucial for fertilisation success. Furthermore, the longevity of gamete viability may influence the potential for egg-sperm interactions. In contrast, *Cystophora torulosa* is monoecious, and therefore may be capable of self-fertilisation. All three species have simple life cycles, with no alternation of generations. A diploid adult produces haploid eggs and sperm which, following fertilisation, develop directly into diploid juveniles (Schiel and Foster 2006). Furthermore, fucoid eggs are relatively large, dense and non-motile (Chapman 1995), and fertilisation and attachment usually occur within only a few hours of gamete release (Brawley *et al.* 1999, Taylor and Schiel 2003). These characteristics provide an excellent model for studies of gamete separation, and subsequent fertilisations success.

In this chapter, I test the effect of distance between male and female gametes on fertilisation success (for *H. banksii* and *D. antarctica*), and whether *C. torulosa* has the ability to successfully self-fertilise. I also test the longevity of *H. banksii* and *D. antarctica* sperm, and if the time after the release of sperm from an adult plant affects fertilisation success.

4.2 Methodology

To test whether *C. torulosa* is capable of self-fertilisation, plants were collected from Wairepo Reef, Kaikoura, during August 2008. Single plants were placed into separate bags, and each plant was stimulated to release its gametes onto plates in separate containers. Propagules released from multiple plants were also settled onto plates as controls (five plants settled onto each plate).

To test the effect of gamete separation on the fertilisation success of *H. banksii* and *D. antarctica,* active sperm were placed at varying distances from viable eggs in shallow, still water. Fertilisation success was measured as the percentage of eggs that had fertilised and elongated after 24 hours.

Algae were collected from Wairepo Reef (for *H. banksii*) and Seal Reef (for *D. antarctica*) during August 2007 and 2008, and washed in seawater to remove any gametes or zygotes that may have attached to the plants. Male and female *D. antarctica* were differentiated in the field (conceptacles are visibly different) and placed into separate zip-lock bags. Male and female *H. banksii* are not easily differentiated in the field, so each plant was placed into a separate zip-lock bag and differentiated following gamete release by the colour of the gametes they released (orange sperm and green eggs). To stimulate gamete release, the samples were refrigerated at 4°C for 24 hours, and then exposed to light at room temperature for 30 minutes. Dense suspensions of sperm and eggs were prepared separately by placing male and females plants into separate containers. Samples were then immersed in 500ml of filtered seawater, and agitated to wash the gametes from the samples.

Fibrolite (‘Hardiflex™’) plates (5 x 5cm) were positioned at opposite ends of shallow trays of varying lengths (5cm, 10cm, 25cm, 50cm, 100cm, 200cm). Trays were washed and filled with seawater (6cm depth) prior to each experiment, and there were three replicates of each treatment (distance).

Using a pipette, 2ml of eggs were placed in the centre of one plate in each tray. The pipette was then changed, and 2ml of sperm was placed on the centre of the plate at the opposite end of each tray. For each experiment, three replicates of two control treatments were also prepared. These were 3 control plates containing 2ml of eggs and no sperm, and 3 control plates containing 2ml of sperm pipetted directly on top of 2ml of eggs.

The longevity of *H. banksii* and *D. antarctica* sperm was tested by releasing 1ml of sperm into 100ml petri dishes filled with seawater, and adding 1ml of eggs after 0, 15, 30, 45, 60, 75, 90, 105 and 120 minutes.

For all experiments, plates containing eggs were examined after 24 hours using a compound microscope and an external light source to determine if fertilisation and elongation had occurred. All fertilised and unfertilised eggs were counted to determine the percentage of eggs fertilised. Each experiment was repeated 3 times for each species.

4.3 Results

No eggs were fertilised when released from single *C. torulosa* plants. However, eggs were fertilised when gametes were released from multiple plants.

The distance between male and female gametes of dioecious *H. banksii* and *D. antarctica* had a significant effect on reproductive success ($F_{6,28} = 58.91$, $p<0.001$; Table 4.1a). The percentage of eggs fertilised decreased with increasing distance between male and female gametes. For *H. banksii*, 79% of eggs were fertilised at 0cm, but at 25cm fertilisation was reduced to 38% (Fig. 4.1a). The percentage of fertilised eggs was not significantly different between species ($F_{1,28} = 5.52$, $p=0.07$), and c. 5 to 15% of eggs were fertilised when gametes were separated by 200cm (the maximum distance tested) in shallow still water.

In sperm longevity experiments the sperm released from *H. banksii* and *D. antarctica* successfully fertilised over 30% of eggs after 120 minutes (the maximum time tested) (Fig. 4.1b). However, the percentage of eggs fertilised decreased with increasing time for both species ($F_{8,36} = 146.39$, $p<0.001$; Table 4.1b). Approximately 80% of eggs were fertilised at time zero, but after 1 hour of sperm release this was reduced to less than 40%.

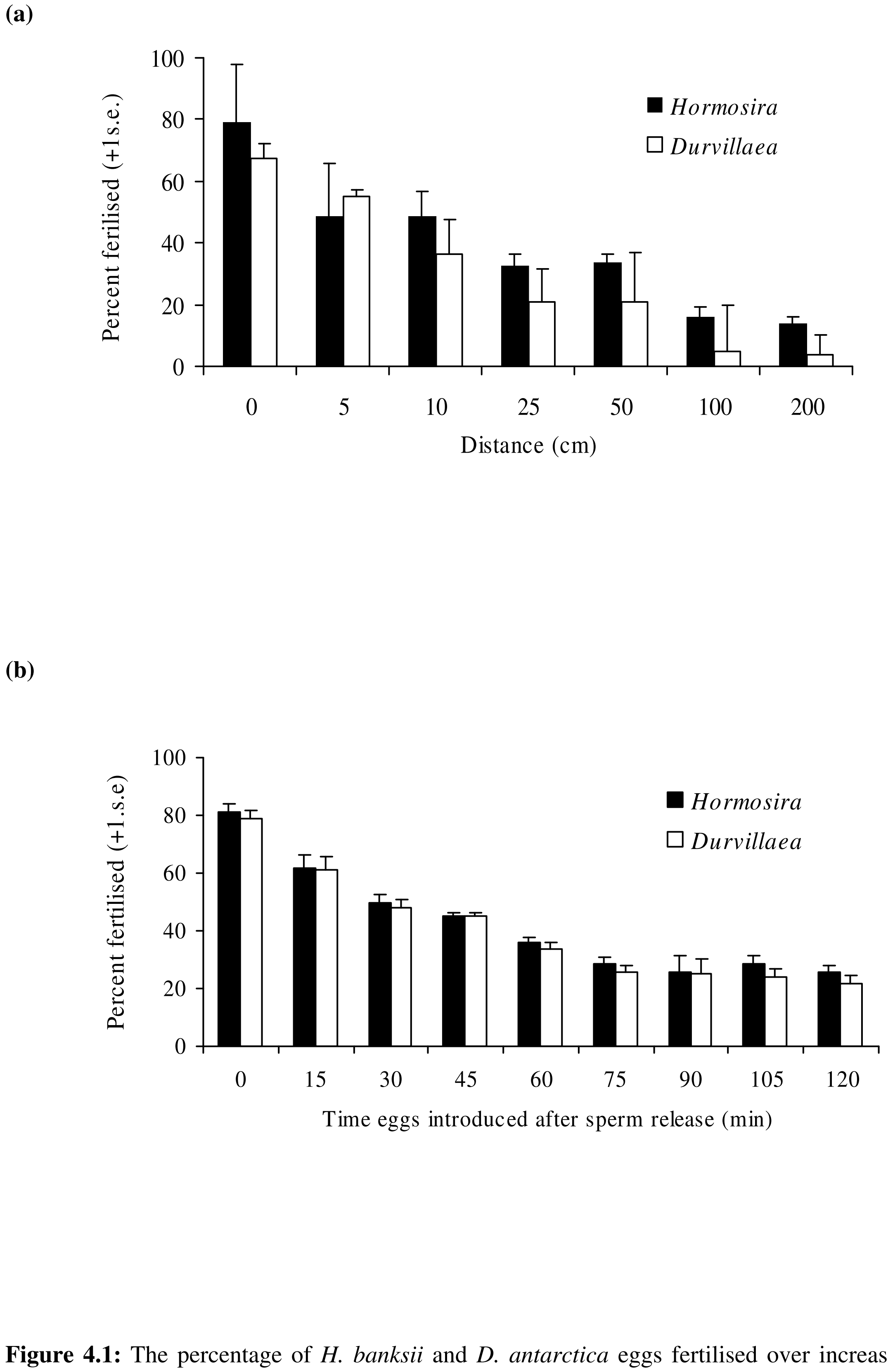


Figure 4.1: The percentage of *H. banksii* and *D. antarctica* eggs fertilised over increasing distance between male and female gametes (a) and over increasing time following sperm release (b). In each case, n= 3 replicates.

Table 4.1: ANOVA on the effect of the distance between male and female gametes of *H. banksii* and *D. antarctica* (a), and the effect of the time after release of *H. banksii* and *D. antarctica* sperm (b), on the percentage of eggs fertilised**.**

(a)

Effect	**df**	**MS**	**F**	**p**
Distance	6	3847.152	58.907	**0.000**
Species	1	360.548	5.521	0.070
Distance x Species	6	138.568	2.122	0.082
Error	28	65.308		

(b)

Effect	**df**	**MS**	**F**	**p**
Time	8	2928.70	146.39	**0.000**
Species	1	189.02	9.45	0.060
Time x Species	8	24.69	1.23	0.308
Error	36	20.01		

4.4 Discussion

Gametes released from single plants of monoecious *C. torulosa* failed to produce viable zygotes. This suggests that, at the time of the experiment, *C. torulosa* was incapable of self-fertilisation and, therefore, no more suited to dispersal by drifting than dioecious species as more than one plant would be required at a new location for fertilisation to occur. Although *C. torulosa* may have the potential to self-fertilise, mechanisms to prevent self-fertilisation can prevent reductions in fitness associated with inbreeding depression. Even if self-fertilisation does occur, fitness can often be decreased in later life stages, and result in decrease survival, growth and fecundity. For example, Raimondi *et al.* (2004) found self-fertilised *M. pyrifera* produced fewer zygotes, had decreased survivorship to adulthood, developed significantly fewer reproductive structures and were subsequently less fecund, compared to outcrossed individuals.

Experiments testing the fertilisation success of dioecious *H. banksii* and *D. antarctica* over increasing distances between gametes showed that fertilisation decreased with increasing distance between male and female gametes. This is likely to result from the dilution of sperm as it diffuses over increasing distances from the source location. Despite this, significant fertilisation occurred when male and female gametes were up to 2m apart, which was the maximum distance tested. Compared to laminarians, this is a considerable distance. Reed (1990) found a minimum settlement density of at least 1 spore mm^{-2} was required for the successful recruitment of *Macrocystis pyrifera* and *Pterygophora californica*, due to the maximum distance that can separate male and female gametophytes for fertilisation to occur.

Chemical cues for gamete location, and the morphological and physiological adaptations of gametes, such as their motility and longevity, are known to influence fertilisation success across many taxa of algae (Brawley 1992, Brawley *et al.* 1999, Santelices 2002). Sperm attractants have been isolated and identified in several species of brown algae, including *H. banksii* and *D. antarctica*, but these are unlikely to facilitate fertilisation over distances as great as 2m, as pheromones appear to function effectively only over short distances not exceeding 1mm (Muller *et al.* 1985). Despite this, in my experiments, sperm were clearly able to swim actively over significant distances in shallow still water. Consequently, the longevity of sperm is likely to influence the distance over which fertilisation can occur. In my experiments, both *H. banksii* and *D. antarctica* sperm remained viable for 2 hours. This characteristic greatly improves the probability of successful egg-sperm interactions over greater distances, even as gametes get diluted in nearshore waters. However, sperm longevity may be influenced by the distance travelled, and in these experiments sperm were confined within $45cm^2$ areas (petri dishes). Furthermore, this method may be insignificant under more turbulent flows, where microscopic sperm are likely to be transported as passive particles in viscous ocean currents. Therefore, the reproductive success of dioecious species will be influenced by the environmental conditions at the time of release.

Gamete release, in natural conditions, often occurs on days with lower water motion (Serrao *et al.* 1996), during low-tide (Brawley *et al.* 1999) and at slack high tide (Berndt *et al.* 2002). Consequently, although my experiments were laboratory-based, these results may be representative of fertilisation distances in the field, during the calm conditions under which gamete release occurs. Several studies have found that decreased water motion triggers synchronous gamete release in fucoid algae (Brawley and Johnson 1992, Pearson and Brawley 1996, Serrao *et al.* 1996, Johnson and Brawley 1998, Serrao *et al.* 1999, Berndt *et al.* 2002), and *H. banksii*, *D. antarctica* and *C. torulosa* have been observed releasing gametes at low tide during calm conditions (Schiel and Taylor 1999, Pers. Obs.).

The synchronous release of gametes from a large source population is likely to concentrate gametes in the water column and reduce the effects of dilution. This may serve to maximize egg-sperm interactions and the probability of successful fertilisation. In my fertilisation distance experiments, using relatively small amounts of sperm and eggs, dilution of sperm is likely to have occurred rapidly after release, especially if sperm attractants were diluted and sperm radiated out from the source. However, under natural conditions, large amounts of beach-cast algae and local populations of attached algae have been observed to release synchronously (Pers. Obs.), perhaps concentrating gametes and reducing the effects of dilution. Some gentle mixing of the water column may further increase the chances of interactions by bringing male and female gametes of dioecious species together (Denny and Shibata 1989). However, the probability that male and female plants will arrive in sufficient abundance, or near a previously established population for synchronous release to be effective, is likely to decrease with distance from the source population.

The reproductive success of species that exhibit external fertilisation depends on high concentrations of gametes, which can only be achieved in the presence of many gamete releasing conspecifics (Thiel and Gutow 2005b). Furthermore, even if fertilisation is possible, subsequent recruitment into a viable population may not be. A minimum density of settlement may be required to produce and maintain a viable population. For example, *H. banksii* requires >1 recruit cm^{-2} to produce a closed canopy, which requires approximately 250 – 750 settlers cm^{-2} (Schiel 2004). Therefore, large rafting species such as *Macrocystis pyrifera* and *Durvillaea antarctica* may have the greatest potential for fertilisation and recruitment at distant sites, as these species can tangle together and accumulate, forming dense clumps of several plants. This may increase the likelihood of successful reproduction by increasing the chance of male and female plants arriving in close proximity. Furthermore, by concentrating gametes with synchronous release from several large plants, subsequent settlement densities may be increased. Rafts of *M. pyrifera* have been reported to consist of more than 200 individual plants (Helmuth *et al.* 1994), whereas smaller species, such as *H. banksii*, are likely to become separated in the drift, and be sparsely distributed in the open ocean.

While disturbance events such as storms can increase the abundance of detached algae, and hence, the numbers arriving at a distant site, most drifting algae caught in coastal current systems following storms are cast up on nearby shores within days of detachment. Therefore, although storm events may favour fertilisation success by ensuring large amounts of algae are cast up together, most beach-cast material is likely to have originated from nearby source populations, and may be more important for short to medium range dispersal, rather than dispersal over oceanic scales. Furthermore, most drifting algae are likely to end up beach-cast, high on the shore, and whether gametes and zygotes are able to disperse to suitable habitats lower on the shore following release is not known. Despite this, beach-cast *H. banksii*, *D. antarctica* and *C. torulosa* can continue to release viable propagules for 7 to 14 days (Chapter 2). The ability of gametes and fertilised eggs to then disperse to suitable habitats lower on the shore is likely to be influenced by very nearshore wave-driven currents (Shanks *et al.* 2003).

Gametes may also reach suitable habitat when drift algae are deposited lower on the shore. Incoming tides and onshore winds may move drifting algae onshore, and the subsequent outgoing tide can then drop this drift lower on rocky reefs, where the potential for suitable habitat is increased (Chapter 3). Although beach-cast algae is usually sparsely distributed lower on the shore (Pers. Obs.), there is the potential to fertilise with gametes released from attached populations, which could lead to successful recruitment. However, there may be genetic costs associated with outbreeding depression, which result from crossing with individuals from distant, genetically separated, populations (Brown 1991, McKenzie and Bellgrove 2006).

The importance of outbreeding depression after arrival at new locations is largely determined by the dispersal capabilities of a species. Species with limited dispersal will have reduced gene flow between populations. This may result in outbreeding depression if fertilisation occurs between individuals from distant populations, if the genetic variability within populations is low (Brown 1991). McKenzie and Bellgrove (2006) found that outbreeding was not evident in experiments testing the fertilisation success of *H. banksii* from distant populations, suggesting long-distance dispersal by drifting, and successful fertilisation and recruitment at distant sites had occurred. However, as with inbreeding depression, the effects of outbreeding may be evident in later life stages.

Summary

Following the onshore transport of reproductively viable drifting algae, fertilisation is required in order to recruit into a new population. Monecious species may be more suited for dispersal by drifting because only one plant may be required at a new location for possible fertilisation. However, in this study, gametes released from single plants of monoecious *C. torulosa* failed to produce viable zygotes. In contrast, dioecious species require both a male and female plant to arrive together at a new location, and gametes must be in close enough proximity for fertilisation to occur. I found that *H. banksii* and *D. antarctica* can successfully fertilise when gametes are separated by up to 2m in still water, and sperm that were viable for 2 hours after release from adult plants, which may facilitate fertilisation and recruitment at distant sites.

Chapter 5 - General Discussion

5.1 Dispersal by drifting: the influence of species characteristics and nearshore processes

Although dispersal by reproductively viable adults is widely accepted, there have been few demonstrations of how this may occur, and how the ability to disperse by drifting can be influenced by species characteristics and nearshore processes. In this thesis, the relative abilities of three species of fucoid algae (*Hormosira banksii*, *Durvillaea antarctica*, and *Cystophora torulosa*) to disperse as drifting adult plants was examined, and related to nearshore processes and species characteristics. I found that offshore winds and outgoing tides are particularly favourable for the offshore transport of drifting algae following detachment, and that detached algae can continue to release viable propagules for a considerable length of time adrift. Furthermore, fertilisation can potentially occur across relatively large distances between male and female gametes of dioecious species, compared to laminarians. There were, however, significant interspecific differences in dispersal capabilities.

Successful long-distance dispersal of drifting algae depends on the completion of several factors, including the ability to move offshore following detachment, the reproductive longevity of algae while adrift and when beach-cast on the shore, the ability to move back onshore to a new and suitable habitat, and subsequent fertilisation and recruitment at new and distant locations. However, few studies have tested these factors experimentally and those that have often focused on single factors (Harrold and Lisin 1989, Macaya *et al.* 2005). Furthermore, most direct evidence for the effectiveness of drifting comes from studies of *Macrocystis* (Harrold and Lisin 1989, Hobday 2000a, 2000b, Macaya *et al.* 2005, Hernandez-Carmona *et al.* 2006), and fucoids are poorly represented. Consequently, the relative importance of long-distance dispersal by drifting is largely unknown.

Dispersal by drifting

The movement of drift offshore after detachment

The first factor influencing the dispersal potential of a species is the ability to move offshore after detachment from rocky reefs (Fig. 5.1). The degree of connectivity between populations will be influenced by the frequency of offshore dispersal events, and by the abundance of drift that moves out of the nearshore environment, to the point where long-distance dispersal could potentially occur. Despite this, no studies have tested the ability of detached algae to move offshore after detachment.

Hobday (2000a) defined a 'successful connection event' between populations to be GPS drifters that were deployed less then 10km from the coast, ending up less then 5km from the coast, but none of these drifters originated from the shore. However, for drifting algae to connect populations successfully, they must move from their point of detachment on the shore, through the turbulent nearshore environment, and into nearshore currents. In my study, periods of onshore winds and incoming tides were particularly favourable for the movement of drift onshore, where it was likely to be beach-cast within one tidal cycle. This may be important for local connectivity, and maintain gene flow within populations. In contrast, offshore winds and outgoing tides were highly favourable for the movement of detached algae offshore, to the point where long-distance dispersal could potentially occur. However, the ability to move offshore varied between species.

The influence of these nearshore processes depended on species characteristics, specifically the buoyancy of the drifting species. My results indicate that benthic drifting algae with limited buoyancy, such as *C. torulosa*, are likely to be influenced by currents moving in different directions to those on the surface and are, therefore, unable to take advantage of favourable conditions for offshore dispersal. Benthic drifting species are also likely to have slower drift velocities, and travel shorter distances, due to entanglement in the heterogeneities of the substratum. Buoyant species, such as *H. banksii* and *D. antarctica*, appear to have greater potential for offshore transport. I found that the velocities and displacement of surface drifting species can occasionally transport drift offshore at relatively high speeds, to the point where long-range dispersal could potentially occur.

Dispersal by drifting

Following offshore transport, drifting algae have the potential for long-distance dispersal. Successful dispersal depends on the ability of drifting algae to remain reproductively viable while adrift. Two studies have tested the reproductive viability of drifting algae, and both were done on *Macrocystis pyrifera* (Macaya *et al.* 2005, Hernandez-Carmona *et al.* 2006). Hernandez-Carmona *et al.* (2006) found that drifting reproductive *M. pyrifera* continued to produce viable zoospores as long as sori were present, which could be up to 125 days.

However, the ability of fucoid algae to continue to release viable propagules while drifting, and whether reproductive longevity varies between species, had never been tested.

My results showed that drifting fucoid algae can continue to release viable propagules for weeks or months while drifting. Furthermore, the reproductive activity of detached drifting plants was no different to that of attached onshore populations. However, the survival and reproductive longevity of drift is likely to be influenced by environmental conditions, such as light (Jokiel 1980), nutrient levels (Edgar 1987) and grazing (Vandendriessche *et al.* 2007), and can vary between species.

Some species may be more susceptible to degradation by grazing, and benthic drifting species may have decreased reproductive longevity due to reduced light deeper in the water column. This may worsen with dispersal away from coastal areas, into deeper waters. For example, although *C. torulosa* continued to release viable propagules for 43 days, there were significantly fewer gametes released by day 36. This could be an indication of a reduction in reproductive activity, which was likely due to *C. torulosa* drifting lower in the water column, and extensive grazing by amphipods. Despite this, my results suggest that detached algae can continue to release viable propagules for weeks or months while adrift. This has important implications for the dispersal potential of these species, and their subsequent recruitment capabilities. However, before reproductive drift can release gametes at a distant site, movement back onshore, to a new and suitable habitat is required.

Movement onshore

Drifting algae can be transported onshore, where it will most likely become beach-cast, immediately following detachment or after dispersal offshore. My results show that onshore winds and incoming tides favour the onshore transport of drift. The subsequent outgoing tide, during onshore winds, may deposit drifting algae lower on the shore, where the likelihood of finding suitable habitat is increased. Slicks produced by internal waves may also facilitate the onshore movement of drift material (Kingsford and Choat 1986). Previous studies have found drifting algae accumulate within slicks (Kingsford and Choat 1986) and although the abundance of algae within slicks was not specifically tested in my study, I observed a similar pattern in transects around Kaikoura and Banks Peninsula. The onshore movement of drifting algae accumulated within slicks may have implications for colonisation at a new location by concentrating algae in small areas, which can increase the probability of fertilisation and recruitment at distant sites.

The movement of drift within the nearshore environment is also influenced by nearshore bathymetry. Drifters were often seen converging along subtidal cracks and were moved towards the head of bays by wave induced currents. The probability of drifting algae getting trapped in coastal inlets and bays, and eventually becoming beach-cast, is influenced by the bathymetry and geomorphology of the shoreline, but the time drift algae can continue to release viable propagules once beach-cast has not been tested. Furthermore, the frequency of re-suspension of drift algae once beach-cast is also largely unknown.

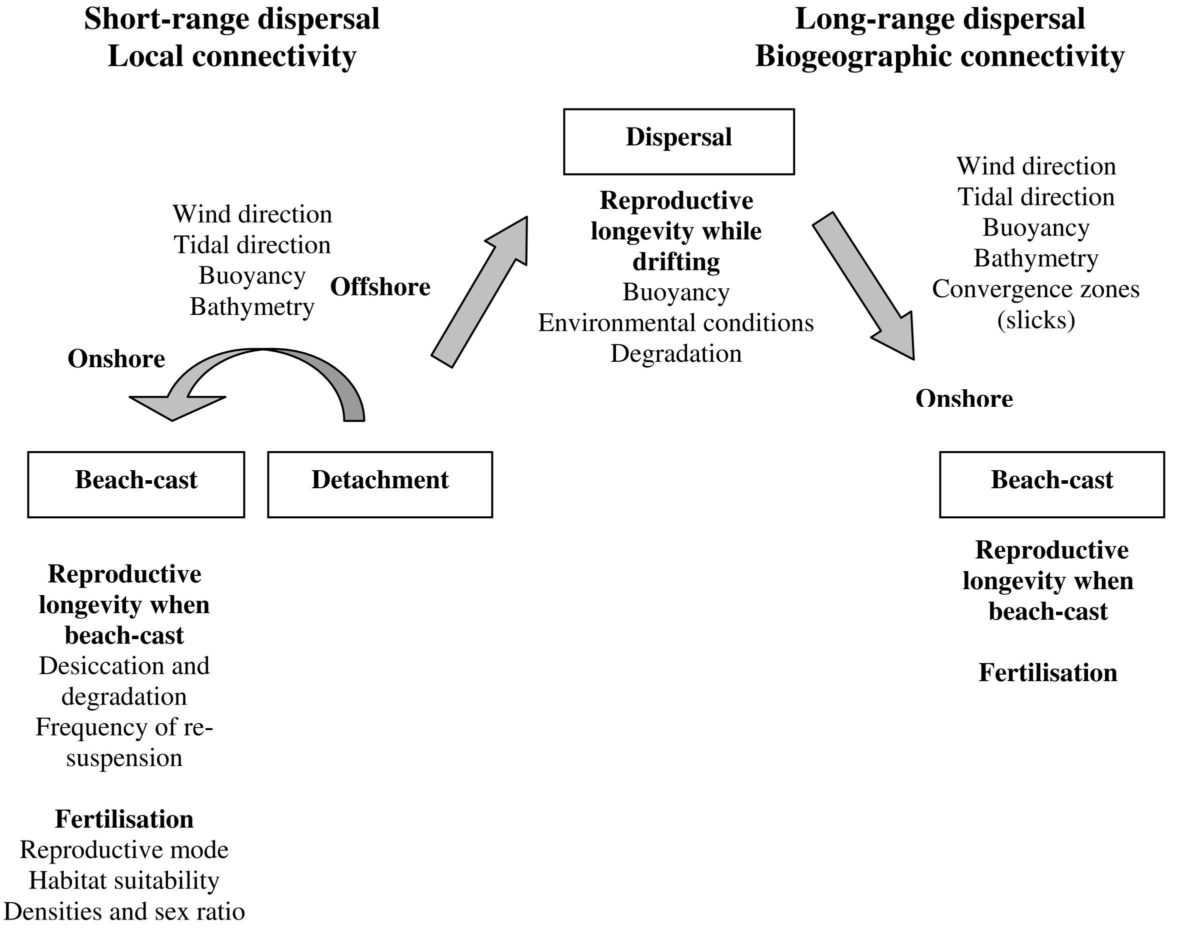


Figure 5.1: Schematic overview of the processes involved in dispersal by drifting adult plants (black boxes), the experiments done relating to these processes (in bold), and the factors found to influence these processes.

Beach-cast drift

I found that detached algae can be transported offshore from release points relatively high on the shore. This suggests that beach-cast algae have the potential to be re-suspended, and transported away from the coast, particularly when neap tides are increasing to spring tide levels. However, this will depend on species characteristics, such as buoyancy, and local environmental conditions. I found that offshore winds and outgoing tides move most detached algae offshore, but that species with limited buoyancy are unable to take advantage of these conditions. Therefore, the ability of surface drifting species to maintain buoyancy when beach-cast will determine their potential for subsequent dispersal offshore. Although some species may degrade and lose buoyancy within days of deposition on the shore, I found that beach-cast *H. banksii* and *D. antarctica* maintained their buoyancy when beach-cast for as long as they were reproductively active.

The reproductive longevity of beach-cast algae is likely to depend on the resistance of a species to desiccation and degradation, as well as the relative ability to photosynthesise in air (Brown 1987). Species with small surface-area-to-volume ratios of the thallus, and adaptations to prevent water loss, such as exuding mucus and storing water, are likely to reduce the speed of desiccation on the shore (Thomas 2002). In my study, beach-cast *C. torulosa* consistently released fewer gametes than attached controls, but *H. banksii* and *D. antarctica* maintained reproductive activity similar to attached controls. This may be due to the evaporation of water from the branched thallus of *C. torulosa*, and the water retaining and mucus releasing properties of *H. banksii* and *D. antarctica.* However, despite this difference, all three study species ceased to release propagules within 14 days of being beach-cast. This suggests there is a relatively small window of opportunity for these species to be re-suspended as drift, before they are essentially lost to the population.

Fertilisation and recruitment at a new location

Following the onshore transport of reproductively viable drifting algae, fertilisation is required in order to recruit into a new population. The ability to fertilise successfully at a new location can vary between species. Species characteristics such as chemical cues for gamete location and the morphological and physiological adaptations of gametes, as well as hydrodynamic conditions, can influence fertilisation success (Brawley and Johnson 1992, Levitan and

Petersen 1995, Levitan and Young 1995, Brawley *et al.* 1999, Santelices 2002). Furthermore, groups of algae exhibit different modes of reproduction. Some species are monoecious and are capable of releasing sperm and eggs and, therefore, may have an advantage because self-fertilisation is possible. However, not all monoecious species can self-fertilise. For example, I found that gametes released from single plants of monoecious *C. torulosa* failed to produce viable zygotes at the time of my experiments, which may prevent reductions in fitness associated with inbreeding depression.

In contrast, dioecious species require male and female plants at a new location for fertilisation and recruitment. Gametes must be in close enough proximity for fertilisation to occur, and the distance between gametes required for successful fertilisation can vary between species. Some algae, such as laminarians, exhibit an alternation of generations, and may require gametes to settle in very close proximity for fertilisation (Reed 1990). However, some species may be capable of fertilisation over much greater distances. I found that *H. banksii* and *D. antarctica* can successfully fertilise when gametes are separated by up to 2m in still water, and sperm was viable for up to 2 hours after release from the adult plant. This may increase the possibility of fertilisation and recruitment at new locations.

Species differences

In this study, *C. torulosa* differed from *H. banksii* and *D. antarctica* in that it did not float within the surface waters. This has obvious implications for long-distance dispersal potential. The position of *C. torulosa* in the water column prevented this species from taking full advantage of conditions favourable for dispersal offshore, and resulted in lower displacement speeds due to entanglement on the substratum. Furthermore, benthic drifting may have contributed to a decrease in reproductive activity of this species, due to less favourable conditions for photosynthesis lower in the water column. Therefore, although benthic drifting species could potentially disperse by remaining within coastal waters, or when entangled with surface drifting species, such species are probably limited to local-scale dispersal, and may contribute to range expansions, maintain gene flow within populations, and connect neighbouring populations (Fig. 5.2).

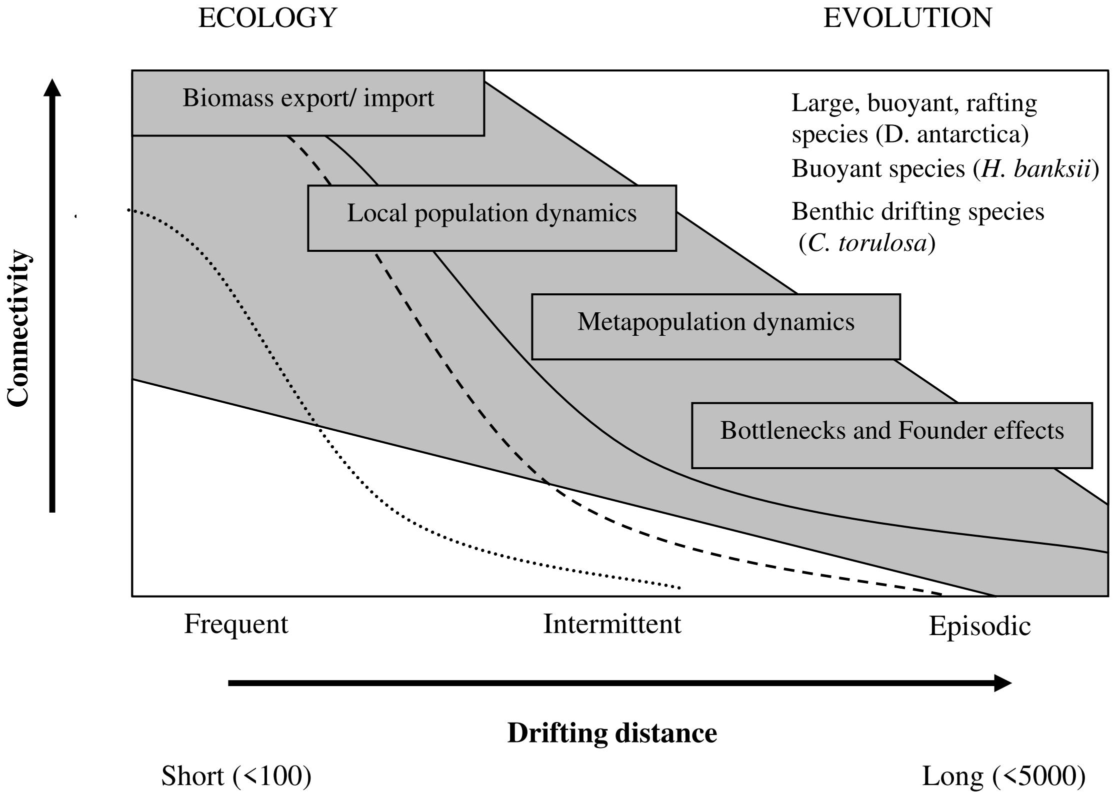


Figure 5.2: Schematic relationship between the frequency and distance of drifting events/routes and the degree of connectivity between populations. The shaded area indicates the number of species and individuals expected to disperse successfully by drifting decreases with distance, and the curved lines indicate the dispersal potential of species with particular characteristics. Adapted from Thiel and Haye (2006).

In contrast, *H. banksii* and *D. antarctica* are positively buoyant, and float within the surface of the water column, enabling these species to take advantage of off-shore surface currents favourable for dispersal away from the coast following detachment. My results suggest that surface drifting species can be transported offshore at relatively high speeds under the right environmental conditions. Furthermore, the reproductive longevity of these species is extensive enough to support long-distance dispersal of over 1000km, which could lead to biogeographic scale connectivity. This could have important ecological and evolutionary consequences for these species.

Rafting species, such as *Durvillaea antarctica* and *Macrocystis pyrifera*, appear to have the greatest potential for long-distance dispersal. Numerous rafts of *D. antarctica* have been observed drifting in the Southern Ocean, often great distances from the nearest source population (Smith 2002). Furthermore, the trans-oceanic distributions of invertebrate species have been attributed to rafting in *Durvillaea* holdfasts (Donald *et al.* 2005). Large algae that become entangled and accumulate, forming rafts of several plants, may also have the greatest potential for fertilisation at distant sites (chapter 4), whereas smaller species such as *H. banksii* may be sparsely distributed in the drift. This suggests that rafting species have the potential for truly long distance dispersal over evolutionary time scales.

Biogeographic distributions

Interspecific differences in dispersal abilities may be reflected in species distributions. *Cystophora torulosa* appears to have limited dispersal capabilities, and is confined to New Zealand and a small area of southern Australia (Tasmania and Victoria) (Womersley 1959, 1964). *Hormosira banksii* has intermediate dispersal abilities and is also confined to New Zealand and southern Australia, but has a more extensive distribution which includes Norfolk and Lord Howe Islands (Adams 1994). In contrast, *Durvillaea antarctica*, a rafting species with the potential for long distance dispersal, has a wide-spread south circumpolar distribution, spanning the Subantarctic Islands, and the southern South American coasts of Chile and Argentina (Adams 1994), and *Macrocystis pyrifera*, the most widely distributed of all kelps, has an extensive amphitropical distribution that spans North and South America, Argentina, South Africa, Australia, New Zealand, and most sub-Antarctic islands (Coyer *et al.* 2001, Macaya *et al.* 2005).

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