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DISPERSAL OF *HORMOSIRA BANKSII* (PHAEOPHYCEAE) VIA DETACHED FRAGMENTS: REPRODUCTIVE VIABILITY AND LONGEVITY[1]

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Drifting, fertile thalli are well documented to be the primary long-distance dispersal vector for many marine macroalgae, but little information about reproductive viability of drift is known. This study examined the reproductive viability and longevity of floating fragments of the intertidal Australasian fucoid *Hormosira banksii* (Turner) Decne. Beach wrack surveys and field experiments were conducted to test the model that long-distance dispersal is achieved in *H. banksii* via floating, fertile fronds. High densities of beach wrack fragments were evident during summer compared to autumn. The majority of beach wrack occurred on sandy beaches rather than rocky shores. Both male and female fragments were present in the beach wrack. Detached fronds were capable of releasing gametes up to 8 weeks after detachment. Beach wrack produced high fertilization rates and recruited successfully onto artificial panels. Results suggest that detached fragments are reproductively viable and that floating, fertile fronds may be an important mechanism for facilitating long-distance dispersal in this species. Nevertheless, the frequency of fronds reaching a suitable habitat and contributing to gene flow between populations, or colonizing new populations, may not be proportional to the total density of beach wrack.

Key index words: **dispersal; drifting; floating; fucoid; gene flow; intertidal; macroalgae; reproduction**

Abbreviation: **ANOVA, analysis of variance**

Long-distance dispersal via drifting, fertile thalli is suggested as being an important mechanism of dispersal for many macroalgal species (van den Hoek 1987, Hales and Fletcher 1988, Norton 1992, Dudgeon et al. 2001, Schiel 2004, Coleman and Brawley 2005a, Macaya et al. 2005, Hernández-Carmona et al. 2006, Silwa et al. 2006). Long-distance dispersal may control the demographics of established marine populations, as well as the dynamics of colonization, range expansion, and genetic exchange (Kinlan and Gaines 2003). Additionally, long-range dispersal promotes genetic diversity within populations while simultaneously decreasing diversity between populations given a high level of gene flow (Lu and Williams 1994, Engelen et al. 2001). *Halidrys dioica* and *Sargassum polyceratium* are capable of long-distance dispersal via their floating reproductive thalli (Lu and Williams 1994, Engelen et al. 2001). As a result, populations of *H. dioica* and *S. polyceratium* have shown a higher genetic diversity (Lu and Williams 1994, Engelen et al. 2001) compared to monoecious seaweeds with limited dispersal [e.g., *Silvetia compressa* (Williams and Di Fiori 1996), *Fucus distichus* (Coleman and Brawley 2005b), and *F. spiralis* (Coleman and Brawley 2005a)], which tend to exhibit lower diversity within populations and high genetic structure among populations.

Specialized gas-filled bladders (pneumatocysts), such as those present on *Sargassum* spp. and *Macrocystis* spp., aid in flotation and thus provide a mechanism for long-distance dispersal. Some seaweeds are known to remain buoyant for weeks to months following detachment (Norton and Mathieson 1983, van den Hoek 1987, Macaya et al. 2005), and many have been reported floating in oceans far from populations of conspecifics (Segawa et al. 1962, Yoshida 1963, Hobday 2000a, Hirata et al. 2001, Thiel and Gutow 2005). During this time, the macroalgal rafts can potentially travel distances up to thousands of kilometers. For example, the brown alga *Durvillaea antarctica* from Western Australia has been found 5,000 km from the nearest shore (Kenneally 1972).

While there is evidence for macroalgal drift, there is little evidence to suggest that drifting macroalgae can remain reproductive following dislodgement. Two known examples are *Macrocystis pyrifera* and *Macrocystis integrifolia.* Drifting sporophylls with sori containing sporangia have been reported for both species (Macaya et al. 2005, Hernández-Carmona et al. 2006). *M. pyrifera* drifters can potentially cover over 890 km while adrift for 125 d and still produce viable propagules (Hernández-Carmona et al. 2006). The reproductive longevity in *M. pyrifera* may be enough to support long-distance dispersal via drifting sporophytes (Hernández-Carmona et al. 2006), thus facilitating gene flow between populations.

Despite this evidence of macroalgal drift, we do not know either how widespread it is among species or how effective this method of dispersal may be. The

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aim of this study was to estimate the reproductive viability, longevity, and recruitment of propagules from drifting material of *H. banksii*, a dominant habitat-forming species common throughout Australasia (Osborn 1948, Womersley 1967, Clarke and Womersley 1981). Like other fucoid species, *H. banksii* is thought to have limited dispersal of propagules, probably restricted to within 10 m (Bellgrove et al. 1997, 2004). However, it has a broad distribution throughout southern Australasia. While there is considerable morphological variation in *H. banksii*, *Hormosira* is currently considered a monospecific genus (Osborn 1948, Clarke and Womersley 1981). Furthermore, we found no evidence of outbreeding depression over distances that may be expected from species with limited dispersal (McKenzie and Bellgrove 2006). Therefore, gene flow may be occurring between populations via drifting fronds and contributing to the broad distribution in this species. Like other taxa known to drift, *H. banksii* has structures that may assist flotation. Thalli of *H. banksii* consist of branched chains of fluid-filled vesicles, contrary to other fucoids where air bladders are small and/or exist only on part of the thallus (e.g., *F. vesiculosus*, Garbary et al. 2006). Pilot laboratory-based floating experiments suggest that fronds and fragments of *H. banksii* are capable of floating (P. F. McKenzie and A. Bellgrove, unpublished data). Furthermore, *H. banksii* fronds make up a significant amount of beach wrack in the east coast of southern New Zealand (Schiel 2004) and are also commonly observed washed ashore around beaches of southern Australia (P. F. McKenzie and A. Bellgrove, personal observations). We tested the model that long-distance dispersal of *H. banksii* is achieved via floating, fertile fronds by specifically investigating the reproductive viability, longevity, and recruitment of propagules of drifting material of *H. banksii*. This study focused on three specific aims: (i) assessing the reproductive viability of beach wrack, (ii) assessing the ability of dislodged fronds to remain reproductive, and (iii) assessing the ability of dislodged fragments to contribute to recruitment.

MATERIALS AND METHODS

Study species. *H. banksii* is a perennial, dioecious alga that commonly forms extensive monotypic beds at midtidal levels of rock platforms (Keough and Quinn 1998). Mature thalli are fertile all year round, and gametes are released during low tide (Osborn 1948, Levring 1949), making *H. banksii* an ideal candidate for conducting reproductive tests anytime during the year. Gametes are exuded from numerous conceptacles located on each mature vesicle (branched chains of vesicles form the thallus). The number of reproductive structures is proportional to the length or weight of the mature frond. Male and female plants are distinguishable by orange sperm and olive green eggs, respectively (Levring 1949). Bellgrove (1992) showed that *H. banksii* is capable of vegetative regeneration with a female to male ratio of 11:1 fronds at a 0.0625 m^2 quadrat scale. However, the sex of *H. banksii* is almost certainly decided at meiosis during gamete production as in other fucoids (Roberts 1966), and given that *H. banksii* has been shown to recruit throughout the year (Bellgrove et al. 2004), a 1:1 ratio of female to male fronds would be expected at the scale of a rocky shore. In this study, fronds were haphazardly collected across the rocky shore at each site to avoid biased sex ratios that would arise by sampling multiple fronds from vegetatively—rather than sexually—generated clumps on smaller spatial scales.

Reproductive viability of beach wrack. Beach wrack surveys were conducted to test the hypothesis that *H. banksii* beach wrack remains reproductively viable. The beach wrack surveys were conducted from 12 sites containing two different habitat types: sandy beach (six sites) and rocky shore (six sites) along the Great Ocean Road, Victoria, Australia (Fig. 1; Table 1). The six sandy beach sites were the sandy beaches located nearest to each rocky shore. Beach wrack of *H. banksii* is present along the Great Ocean Road all year round (P. F. McKenzie, personal observations); surveys were conducted during March and October 2006 to examine the temporal consistency of wrack abundance. At each site, a 100 m × 2 m location was haphazardly selected, and all dislodged *H. banksii* fragments (wrack) were cleared from the sampling area. One week later, at the same location, 100 quadrats (50 cm × 50 cm each) were randomly allocated within the sampling area. Wrack of *H. banksii* in each quadrat was collected. This sampling design allowed an estimation of wrack age by wrack being up to 1 week old (hereafter 1-week wrack). The 1-week wrack from each quadrat was collected in individual airtight bags and transported back to the lab on ice. Total wrack abundance per quadrat per site was assessed by counting both the number of fronds and vesicles. Gamete release was stimulated for 1-week wrack from all 12 sites. Gamete release was stimulated following methods described by Kevekordes and Clayton (1996) to assess the ability of fragments to release gametes. Ability to release gametes was quantified for all tests by the presence of any exuded gametes from the conceptacles of each fragment; the density of gametes per fragment was not recorded. Fertilization success was assessed for each site using a sperm:egg ratio of 50:1 to avoid polyspermy (Kevekordes and Clayton 1996). At random and for each site, 100 eggs were assessed after 1 h to determine whether they had fertilized successfully, following methods described by McKenzie and Bellgrove (2006). Fertilization success was not assessed for a site if only one sex was found or gamete release did not occur. Germination was not scored due to previous work showing no difference between fertilization success after 1 h and gamete development after 14 d for sperm and egg crosses within rocky-shore populations (McKenzie and Bellgrove 2006). Thus, gamete release and fertilization success were considered adequate predictors of viability.

Ability of dislodged fragments to remain reproductive. Experimental tests of the ability of dislodged fragments to remain reproductive were conducted at Crofts Bay, Bay of Islands Coastal Park, Victoria, Australia (−38°37′ S, 142°52′ E; Fig. 1). The sandstone platform was ~300 m in length and 20 m wide and had an extensive bed of *H. banksii*. Dislodged fragments of *H. banksii* were tethered on a rocky shore to test the hypothesis that dislodged fragments remain reproductively viable for long periods. Eighty healthy fronds (~17 cm in length) were haphazardly collected and put into individual polyethylene, extruded, tubular nets (Netpak, Wetherill Park, Australia; mesh size: 3 mm). One end of the net was secured with a cable tie to keep the frond in the net, and the other end was sewn and knotted with a nylon leader (tensile strength: 13.6 kg), 60 cm in length. At the free end, the nylon leader was threaded through a plastic cattle tag and then double knotted around a 10-gauge, stainless-steel, self-tapping countersunk screw (38.1 mm) and attached to the rock platform. Prior to

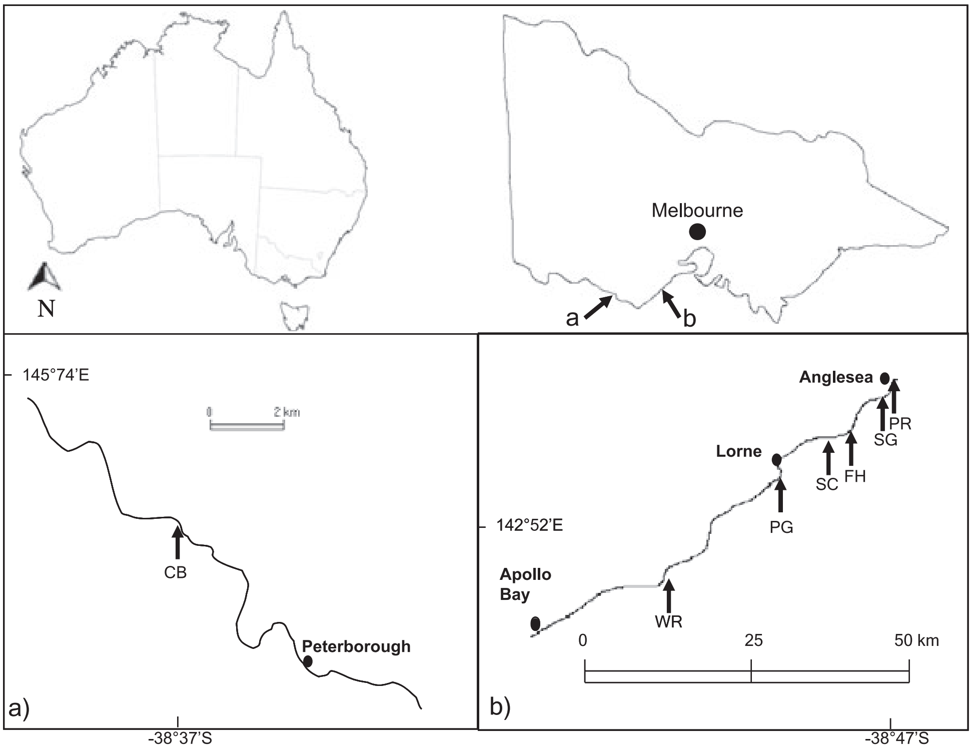

FIG. 1. Location of study sites. (a) Crofts Bay, Bay of Islands Coastal Park, Victoria (CB); and (b) sites located along the Great Ocean Road, Victoria (PR: Point Roadknight; SG: Sandy Gully Beach; FH: Fairhaven Surf Lifesaving Club; SC: Spout's Creek; PG: Point Grey; WR: Wye River).

commencement of the experiment, 20 fronds were haphazardly collected from the rock platform, and gamete release was stimulated to compare initial gamete-release ability with release ability over the period of the experiment. Twenty tethered fronds were then collected every 2 weeks over an 8-week period. All tethered fronds were transported back to the laboratory on ice, and gamete release was stimulated and recorded for each frond. The experiment was conducted twice to assess temporal generality of patterns: during summer 2006/2007 and autumn 2007.

Ability of dislodged fragments to contribute to recruitment. Recruitment of *H. banksii* beach wrack onto artificial substrata was examined to test the hypothesis that beach wrack can contribute to recruitment to established populations of *H. banksii* as effectively as fresh fronds. The experiment was conducted during May 2007 at Sandy Gully Beach, Airey's Inlet. Four treatments were used: (1) beach wrack secured to the rock platform with plastic gutter mesh, (2) fragments freshly dislodged from the rocky shore and secured to the rock platform with plastic gutter mesh, (3) naturally attached (and growing) fronds covered with plastic gutter mesh, and (4) naturally attached (and growing) fronds with no mesh. The third treatment controlled for the dislodgment of fragments (H_0: no difference between treatments 2 and 3). The fourth treatment controlled for any artifact the mesh might have had on recruitment (H_0: no difference between treatments 3 and 4). Fiber-based cement plates (Gyprock, Warrnambool, Victoria, Australia) were used as a standard synthetic substratum for settlement (Taylor and Schiel 2003). Plates were 7 mm thick and were cut into 5 cm × 5 cm squares. All plates were soaked in seawater 1 week prior to commencement to leach potentially toxic compounds. Beach wrack (age unknown) was haphazardly collected during low tide from the sandy beach adjacent to the rock platform prior to commencement of the experiment.

TABLE 1. Grid references for study sites sampled for the reproductive viability of beach wrack surveys.

Site	Grid reference
Point Roadknight, Anglesea	38°28′ S, 144°10′ E
Sandy Gully Beach, Airey's Inlet	38°27′ S, 144°06′ E
Fairhaven Surf Lifesaving Club, Fairhaven	38°28′ S, 144°05′ E
Spout's Creek	38°28′ S, 144°01′ E
Point Grey, Lorne	38°32′ S, 143°59′ E
Wye River	38°38′ S, 143°53′ E

For the dislodged-fragment treatments (wrack and freshly dislodged fragments), fragments were haphazardly separated into 10 replicates (each weighing 200 g) for each treatment. Two artificial panels per replicated treatment (herein experimental unit) were haphazardly positioned within 1 cm of each other and screwed into the rock. For each experimental unit, one 200 g replicate was placed on top of each panel and secured using 20 cm × 30 cm plastic mesh (0.5 cm × 0.5 cm mesh size) and eight 10-gauge, stainless-steel, self-tapping countersunk screws (38.1 mm). Treatments and experimental units were randomized on the rocky shore within an area of ~500 m^2, and experimental units were within 30–100 cm of each other. Fronds were secured directly over the panels to maximize recruitment from experimental fronds and minimize any recruitment from surrounding attached individuals. Trials tagging the experimental propagules (staining) of *H. banksii* proved unsuccessful (J. L. McKenzie and A. Bellgrove, unpublished data), but additional trials have shown limited recruitment at even small distances (10 cm) from a point source (J. L. McKenzie and A. Bellgrove, unpublished data), so we believe that the majority of recruits on the panels came from the experimental fronds.

For the attached frond treatments, panels were placed beneath an estimated 200 g of fronds and secured by mesh for treatment 3 or otherwise left free for treatment 4. Fronds from these treatments were collected at the end of the experiment and weighed to check for weight consistency with the other treatments. There was a consistent weight of fragments across treatments (mean ± SE, 200.25 ± 0.71); therefore, recruitment density was comparable across treatments. Panels were left for a period of 2 weeks to allow for recruitment and were then collected in individual containers (excluding water to prevent disturbance during traveling) and transported back to the laboratory on ice. Microfiltered (0.22 μm; Sterivac Millipore Corporation, Bedford, MA, USA) seawater was added to each container with the two panels from each experimental unit. The panels were then placed randomly in a temperature-controlled cabinet and kept on a 12:12 light:dark (L:D) cycle at 15°C ± 1°C during processing (2 d). Zygotes/germlings on the panels were counted in the laboratory with the aid of a dissecting microscope (Stemi SV6; Zeiss, Jena, Germany).

Statistical analyses. All statistical analyses were conducted using the statistical packages SPSS version 15.0 or SYSTAT version 10.0 (SPSS Inc., Chicago, IL, USA).

Reproductive viability of beach wrack: Frequency of fronds in the beach wrack was compared between the factor habitat (two levels: rocky and sandy) and for each sampling time (two levels: March and October) using Pearson's chi-square test and to test the null hypothesis that sampling time was independent of habitat. Data were compiled by presence/absence data pooled for sandy beach and rocky shore sites for each sampling time. Proportion of wrack releasing gametes between the two habitat types (pooling sites) was also analyzed using Pearson's chi-square test to test the null hypothesis that sandy beach habitats were independent of rocky shore habitats. Proportion of fragments releasing gametes was pooled across sites for each habitat. The assumption of independence and the assumption of no more than 20% of the categories having expected frequencies <5 were both met (Quinn and Keough 2002). Yates corrections were applied to all two-way Pearson's chi-square tests that had only one degree of freedom.

Fertilization success (proportion of fertilized eggs) from wrack collected on the sandy beach habitats was analyzed between each sampling time by one-way analysis of variance (ANOVA) with the factor time (two levels: March and October). The null hypothesis tested was that there would be no difference between March and October. Assumptions of normality and homogeneity of variances were checked with box plots and residual plots (Quinn and Keough 2002). Count data were fourth-root transformed or log transformed, and proportion data were arcsine transformed to meet assumptions where necessary.

Ability of dislodged fragments to remain reproductive: Pearson's chi-square test was used to test the null hypothesis that the observed frequencies (ability to release gametes) were homogenous over weeks (five levels for summer experiment: 0, 2, 4, 6, and 8 weeks; four levels for autumn experiment: 0, 2, 4, and 6 weeks) and ability to release gametes (two levels: release and no release). Data were compiled by the frequency of gamete release for each week for each experiment. The assumption of independence and the assumption of no more than 20% of the categories having expected frequencies <5 were both met (Quinn and Keough 2002).

Ability of dislodged fragments to contribute to recruitment: Differences in recruitment between treatments were compared with a one-way ANOVA, with the factor treatment (four levels: treatments 1–4). The null hypothesis tested was that there would be no difference between treatments. Assumptions of normality and homogeneity of variances were checked with box plots and residual plots (Quinn and Keough 2002). Count data were fourth-root transformed or log transformed, and proportion data were arcsine transformed to meet assumptions where necessary.

RESULTS

Beach wrack surveys. Fragments of *H. banksii* were abundant in the sandy beach wrack, but the abundance differed between March and October (Fig. 2, a and b). Fragments of *H. banksii* were significantly more abundant on the sandy beaches than the rocky shores (Table 2; Fig. 2, a and b; March: $\chi^2_{(1)} = 359.0$, $P < 0.01$; October: $\chi^2_{(1)} = 125$, $P < 0.01$). Vesicles were also more abundant on sandy beaches than rocky shores (Fig. 2, a and b). Although fragments of *H. banksii* up to 1 week old were often abundant in the wrack on sandy beaches and to a lesser extent on rocky shores, only a small proportion of these fragments successfully released gametes (Fig. 2, c and d). Both male and female

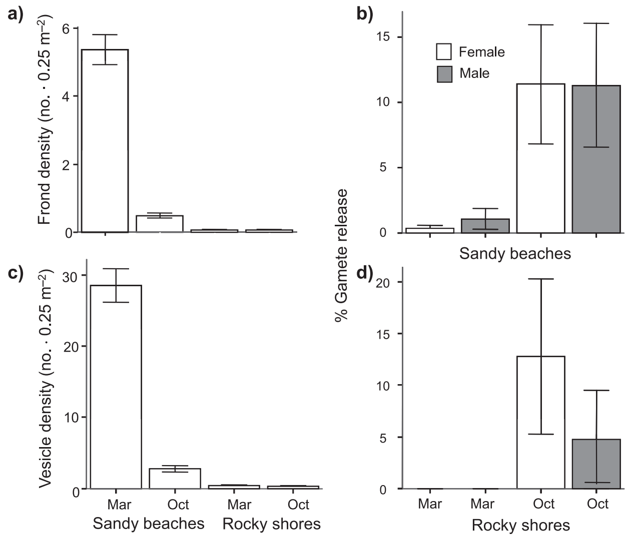

FIG. 2. Mean (±SE) 1-week-old (a) frond density and (b) vesicle density of *Hormosira banksii* collected from the beach wrack on rocky shores and sandy beaches in March and October 2006. Each white bar represents six pooled sites ($N = 600$). Mean (±SE) percentage of female (white bars) and male (shaded bars) fragments of *H. banksii* that successfully released gametes; (c) sandy beaches (six sites pooled) and (d) rocky shores (six sites pooled) during March (M) and October (O) 2006.

TABLE 2. Number of quadrats in which 1-week-old fragments of *Hormosira banksii* were present for sandy beaches and rocky shores ($n = 600$, pooling six sites for each habitat) during March and October 2006.

	Habitat		
Sampling time	Sandy beaches	Rocky shores	Total
March	336	23	359
October	102	23	125
Total	438	46	484

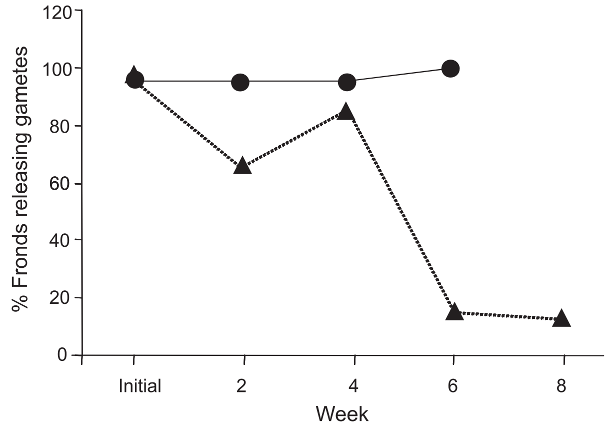

FIG. 3. Percentage gamete release for tethered fronds of *Hormosira banksii* for experiments conducted in summer (triangles and dotted line; $n = 20$ for initial–week 6 and $n = 17$ for week 8 due to loss of replicates) and autumn (circles and solid line; $n = 20$ for initial–week 4 and $n = 12$ for week 6 due to loss of replicates).

fertile fragments (identified by color of exuded gametes) were present in the wrack (Fig. 2, c and d). While gamete release was low, fertilization success of beach wrack on sandy beaches (within-site crosses) was high for both sampling times (82.60 ± 2.39% for March and 77.48 ± 1.51% for October, $F_{(1,39)} = 3.5$; $P > 0.05$). There was insufficient gamete release on rocky shores to perform within-site crosses to assess fertilization success.

Ability of dislodged fragments to remain reproductive. Detached fronds were capable of releasing male and female gametes 8 weeks postdislodgement; however, this ability differed between trials (Fig. 3).

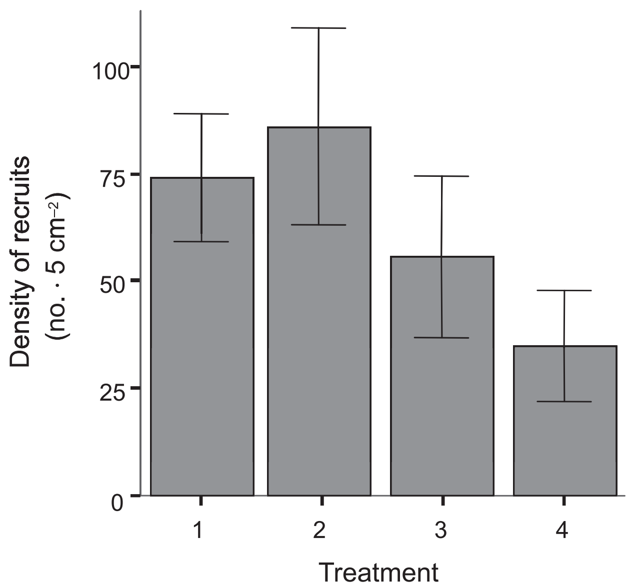

FIG. 4. Mean (±SE) density of recruits of *Hormosira banksii* on artificial panels for four treatments: (1) fronds from beach wrack with mesh, (2) freshly detached fronds with mesh, (3) attached fronds with mesh, and (4) attached fronds with no mesh; $n = 20$.

The chi-square test revealed a significant difference between observed and expected (100%) percentage gamete release for the summer experiment ($\chi^2_{(4)} = 41.4$, $P < 0.01$, Fig. 3) with only 10% of tethered fronds releasing gametes after 8 weeks. When the experiment was repeated in autumn, there was no reduction in fertility over time ($\chi^2_{(3)} = 0.6$, $P > 0.05$, Fig. 3). There were only data for 6 weeks for trial 2 due to loss of tethers.

Ability of dislodged fragments to contribute to recruitment. *H. banksii* successfully recruited to artificial substrata in all treatments, including the treatment using wrack (Fig. 4). Freshly detached fronds with mesh treatment showed the highest recruitment (mean ± SE = 86 ± 23 · 5 cm^{-2}), whereas the treatment with attached fronds and no mesh showed the lowest recruitment of *H. banksii* zygotes (mean ± SE = 35 ± 13 · 5 cm^{-2}). There was no significant difference in recruitment between all treatments ($F_{(3,\ 76)} = 1.56$, $P > 0.05$, Fig. 4), indicating that dislodgment alone did not affect recruitment.

DISCUSSION

This study supports the model that long-distance dispersal of *H. banksii* may be achieved via floating, fertile fronds. Beach wrack of *H. banksii* was reproductively viable by releasing gametes and fertilizing successfully at high rates. Tethered fronds remained reproductively viable for up to 8 weeks. Furthermore, dislodged fragments, including beach wrack fragments, successfully recruited onto artificial substrata. However, the vast majority of the beach wrack in the surveys did not release, and only a small proportion of the total beach wrack was found on rocky shores. The frequency of drifting fronds arriving at distant populations and thus contributing to gene flow is thus likely to be low.

The highest abundance of beach wrack occurred at the end of summer, comparable to drifting fragments of *Caulerpa racemosa* (Ceccherelli and Piazzi 2001). While summer seems to be the ideal time to drift for *C. racemosa* (Ceccherelli and Piazzi 2001), it may not be for *H. banksii.* Gamete release was variable and reduced during summer. If this was the primary time of fragments drifting for *H. banksii,* the chance of contributing to gene flow may be minimal. However, ZoBell (1971) has shown that drift seaweed on sandy beaches at San Diego County had the highest abundance of seaweed during winter compared to the other three seasons surveyed. Furthermore, studies carried out on South African beaches showed that there was a higher abundance of wrack during the winter and a lower abundance of wrack in the summer periods (Koop and Field 1980, Stenton-Dozey and Griffiths 1983). While this time of year would be more suitable for drifting *H. banksii* fragments, greater temporal sampling of beach wrack of *H. banksii* is needed to confirm patterns of abundance.

The majority of beach wrack sampled was found at sandy beaches, which are unsuitable substrata for recruitment of *H. banksii.* Fragments may only be picked up from the source population and subsequently dropped off onto the nearest beach by tidal influences. It is unknown how much resuspension of beach wrack at high tide and longshore drift of fragments of *H. banksii* occurs. Future studies applying molecular markers such as microsatellites may identify the source population of drift, and therefore the amount of longshore drift of *H. banksii* may be determined.

Beach wrack fragments were capable of releasing gametes; however, variation within a sampling time and between sampling times was high. The high variability evident for October may have been due to the beach wrack comprising different ages (e.g., 1- to 7-day-old drift). Older fragments may have been desiccated and exposed to light for long periods, which may have affected the ability to release gametes. The variation in reproductive viability evident between March and October may have been due to the fragments being exposed to warmer conditions (UV exposure) during March compared to October (see comments below on sunburn events).

Only a small proportion of the total beach wrack abundance released gametes; however, gametes were viable and produced high fertilization rates, comparable to rates shown under laboratory conditions with fresh algal material (Gunthorpe et al. 1995, Kevekordes and Clayton 1996, McKenzie and Bellgrove 2006). Despite the evidence of high fertilization rates, the success rate of gametes developing into healthy adults remains unknown. With only a very small proportion of beach wrack releasing gametes and likely high postsettlement mortality (Bellgrove et al. 2004), the number of gametes released from the beach wrack that develop into healthy adults is likely to be minimal. Other studies of algal recruitment have shown that only a small proportion (ranging from $1 \times 10^{-5}\%$–5%) of the total propagules released from the adult developed into visible recruits (Chapman 1984, 1995, Ang 1991). Although the density of beach wrack recruitment was high and recruits appeared healthy after 14 d, the weight of wrack used in the experiment (200 g per replicate) was well above that likely to occur on rocky shores ($\sim$0.2 g · m^{-2}). A higher than natural wrack density was used for this experiment as previous recruitment studies with *H. banksii* showed high mortality rates of zygotes on artificial substrata (A. Bellgrove, J. L. McKenzie, P. F. McKenzie, B. J. Sfiligoj, and D. Williams, unpublished data). Our main objective was to test whether beach wrack was capable of recruitment; therefore, we used a high density to account for potentially high mortality and still allow enough power to detect treatment effects. Another experiment under realistic conditions is the next step in assessing the contribution drift is likely to have to recruitment.

Studies of other detached macroalgae have also showed low propagule release. For example, zoospore production in *M. pyrifera* was reduced following detachment (Hernández-Carmona et al. 2006). However, germination rates were lower (44%–46%; Hernández-Carmona et al. 2006) compared to fertilization rates shown by *H. banksii* (77%–82%). McKenzie and Bellgrove (2006) showed fertilization and germination rates to be comparable for *H. banksii.* In contrast, Macaya et al. (2005) reported high rates of germination of zoospores (80.8%) from floating sporophytes of *M. pyrifera* and *M. integrifolia.* It may be that germination and/or fertilization may vary spatially and temporally as Macaya et al. (2005) and Hernández-Carmona et al. (2006) sampled at different times of the year and surveyed *M. pyrifera* off different coasts.

Reproductive ability differed between the two tethering experiments, possibly because of the different seasons when the experiments were conducted. The first experiment was conducted during a very hot summer (highest recorded air temperature = 41°C) with lower than usual low tides coinciding with peak temperatures. The highest recorded temperature experienced during the previous summer and at the same location was 36°C. Under these warmer conditions, fronds of *H. banksii* became sunburnt. This species is highly susceptible to sunburn during periods of high UV radiation (Keough and Quinn 1998, Schoenwaelder 2002). While it is reported that sunburn only penetrates a few cells deep (Schoenwaelder 2002), it may affect reproductive output. During the period of the first tethering experiment, thalli on the shore and fronds in the tethers became dark brown in color (sunburnt) and very dry and brittle. The severity of the environmental conditions over the summer period likely affected the reproductive ability of *H. banksii* as tissue surrounding the conceptacles was damaged. Furthermore, fertilization rates of *H. banksii* have been shown to vary seasonally, particularly during the warmer months (Gunthorpe et al. 1995). To assess the influence of the sunburn events on the generality of this pattern, an additional experiment was conducted in autumn once *H. banksii* had recovered from the sunburn and the air temperature had decreased. The autumn experiment showed a more consistent pattern of gamete release over the experimental period compared to the summer experiment. Gamete release during the autumn experiment was high over the 6-week period. Even though the autumn experiment did not continue for the same duration as the summer experiment (8 weeks) due to loss of tethers (only 6 weeks), it is expected that after 8 weeks the ability of fronds to release gametes would still be high. Additional tethering experiments are the next step to further examine the threshold of fertility of dislodged fronds and include tethered fronds further offshore.

Some biases may arise from the method used to tether fronds of *H. banksii* to the rocky shore compared to naturally floating fronds. For example, mechanical abrasion on the tethered frond or the tubular net encasing the frond may have an impact on the ability of the frond to release gametes. Such biases have been considered in other tethering seaweed studies where biases may potentially over- or underestimate aging rate or drifting time of kelp rafts (Hobday 2000b, Hernández-Carmona et al. 2006).

Reproductive structures on drift algae seem to be a common occurrence for many species within the Lessoniaceae, Fucaceae, and Sargassaceae families (Macaya et al. 2005). Together with this knowledge and the results of this study, it appears likely that long-distance dispersal may occur via fertile, floating algae. A wide range of macroalgal species are washed up around the world's beaches; some are found many kilometers away from their nearest source population (van den Hoek 1987). Given that the dispersal of most fucoid propagules seems to be limited (Santelices 1990, Kendrick and Walker 1991, 1995, Bellgrove et al. 1997, 2004), floating fragments may be an important dispersal mechanism and may maintain gene flow between populations. Floating, fertile fronds of *H. banksii* may only need to be occasionally successful to enable gene flow between populations (Valero et al. 2001, Billot et al. 2003, McKenzie and Bellgrove 2006) and to sustain its broad distribution. Future studies investigating genetic diversity over the broadscale distribution of *H. banksii* using genetic markers may give valuable insight into gene flow and long-distance dispersal in this species. Additionally, studies into the importance of a conspecific canopy to successful recruitment of *H. banksii* are needed to understand the likelihood of drifting, fertile fragments establishing new populations.

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