



Wave-related mortality in zygotes of habitat-forming algae from different exposures in southern New Zealand: the importance of ‘stickability’

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Received 8 January 2002; received in revised form 12 December 2002; accepted 7 February 2003

Abstract

Using field and laboratory experiments, we investigated the relative ability of zygotes of three species of habitat-forming large brown algae from southern New Zealand to survive wave action and remain attached after settling times of 1, 6, and 12 h. Zygotes of *Hormosira banksii* (Turner) Decaisne and *Cystophora torulosa* (R. Brown) J. Agardh, intertidal algae common on sheltered and semi-protected shores in southern New Zealand, had between 24% and 35% survival 1 h after settlement and exposed to a single wave in the lab and field. In contrast, *Durvillaea antarctica* (Chamisso) Hariot, an exposed-shore species, had up to 75% survival under the same conditions. Survival increased with post-settlement time for all three species. When given 6 h to attach under the same conditions, the survival of *Hormosira* and *Cystophora* zygotes ranged between 50% and 60% and between 80% and 90% when given 12 h to attach. *Durvillaea*, in contrast, had between 90% and 100% survival at both 6- and 12-h setting times. In other experiments, *H. banksii* and *D. antarctica* zygotes were given either 1, 6, or 12 h to attach and then placed for 12 h into sites within three levels of wave exposure (sheltered, intermediate and exposed). Survival of *Hormosira* zygotes given 1 and 6 h to attach was poor, ranging from 1% to 8%. If given 12 h to set, however, 5–8% of *Hormosira* zygotes survived, even at the exposed sites. Under similar conditions, *Durvillaea* survival was significantly higher, ranging from 70% to 100% at all post-settlement times, in sites of all exposures. Wave action clearly affects the ability of sheltered shore species to settle in exposed sites. However, our study highlights the importance of factors other than wave action in determining the distribution and abundance of post-settlement stages of *D. antarctica* across exposures.

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Keywords: Attachment; Habitat-forming algae; Macro-algae; Settling time; Wave action; Wave exposure; Zygotes

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1. Introduction

The ability of early life stages to remain attached to rocky substratum following settlement is fundamental in determining the distribution and abundance of benthic populations. Of the numerous environmental and biological factors that affect the distribution and abundance of intertidal populations, wave action is one of the more important and has received much attention over the last 20 years (Hurd, 2000). The combined indirect and direct hydrodynamic effects of wave action on nearshore intertidal biota are often grouped under the term ‘wave exposure’ (Ballantine, 1961; Dalby et al., 1978; Menge and Sutherland, 1987; Denny, 1995). Direct effects of wave forces on intertidal organisms can include damage, detachment and displacement (Vogel, 1984; Denny, 1995). Indirect effects can involve interactions with sediment, logs, rocks and adult populations (Dayton, 1971; Paine and Levin, 1981; Sousa, 1984; Schiel, 1985, 1988). Across exposures, competition and predation form the basis of models of on-shore processes (Connell, 1961; Menge, 1978; Menge and Sutherland, 1987; Menge and Farrell, 1989; Menge et al., 1994). Until recently, however, many of the specific processes linking patterns of species distributions and abundance to wave action had not been quantified or examined experimentally (Vadas et al., 1990; Denny, 1995).

Significant progress has been made in understanding the effects of wave forces on the size, distribution and abundance of the larger stages of intertidal organisms (e.g. Koehl, 1984; Vogel, 1984; Denny et al., 1989; Denny, 1987, 1995; Carrington, 1990; Gaylord, 1999). However, much less is known about effects on the microscopic early life stages. The period between settlement and recruitment can be critical in determining the distribution and abundance patterns of marine populations (Norton, 1983; Underwood and Denley, 1984). In barnacle populations, for example, recruitment largely reflects settlement, but this relationship can be density-dependent and highly variable (Caffey, 1985; Connell, 1985; Gaines and Bertness, 1992). The relationship between settlement patterns and recruitment is largely unknown for marine algae (Chapman, 1995), although Kendrick and Walker (1995) found that >99% of embryos of *Sargassum* spp. died within 2 months of the end of the reproductive season. However, the effect of wave forces on the attachment and survival of algal zygotes has been tested in a few studies. For example, Vadas et al. (1990) used zygotes of *Ascophyllum nodosum* (L.) Le Jolis to test wave-related mortality following settlement. Ninety-nine percent of zygotes settled for 15 min on smooth pottery plates were removed by a single low-energy wave. Even with post-settlement times up to 4 h and the provision of refuges, 75–90% of zygotes of *Ascophyllum* were detached after a single low-energy wave. In contrast, *Hormosira banksii* (Turner) Decaisne zygotes remained attached when exposed to a jet of water from a pipette 5 h after settling (Forbes and Hallam, 1979).

Algal zygotes use a range of adhesive mechanisms to attach to substrata. In general, the attachment phase of nonmotile spores is characterised by the secretion of mucilage that hardens over time to facilitate adhesion (Fletcher and Callow, 1992). Variation in the amount of mucilage and the time taken for it to harden could have important ecological consequences. For example, greater amounts and a faster setting time of mucilage could benefit epiphytic species or those species settling in high wave-energy environments. Moorjani and Jones (1972) found that the epiphytic coralline alga *Jania* had a stronger and

faster attachment than did the benthic *Corallina*. Similarly, the slow and weak attachment of early life stages of the large brown alga *A. nodosum* may explain its absence from high wave-energy situations (Vadas et al., 1990).

There are clear differences in the dominant habitat-forming algae across exposures on the intertidal platforms of the eastern coast of southern New Zealand (Morton and Miller, 1973; Schiel and Taylor, 1999). In wave-exposed situations, the dominant alga is the large bull kelp *Durvillaea antarctica* (Chamisso) Hariot, the biomass of which can reach 80 kg/m². However, the distribution of *Durvillaea* does not extend to more sheltered shores, which instead are dominated by fucalean algae such as *Cystophora torulosa* (R. Brown) J. Agardh on the lower shore and *H. banksii* (Turner) Descaisne on the mid-shore. With the exception of small plants in cracks and tide pools (Osborn, 1948), *H. banksii* and *C. torulosa* are not found in wave-exposed situations.

This study examines the possibility that the observed patterns of distribution and abundance of habitat-forming large brown algae are related to the ability of their zygotes to stick and remain attached when exposed to varying degrees of water motion. For intertidal species, adhesion must occur within the context of tidal cycles. These are semi-diurnal in New Zealand, with two sets of high and low tides of approximately equal magnitude daily. We hypothesized that zygotes of *C. torulosa* and *H. banksii*, characteristic of more sheltered situations, would not attach as quickly and would not survive wave action as well as the exposed-shore species *D. antarctica*. The null hypothesis of equal attachment of the species is tested under artificial and natural wave conditions and over various post-settlement times.

2. Materials and methods

In this study, we did two sets of experiments. The first of these were “single-wave” experiments, done in both the laboratory and the field. These tested the immediate consequences of the least amount of wave action on the ability of algal zygotes to remain attached. These were done as a comparison with another published study on algal zygote attachment (Vadas et al., 1990). The second set of experiments (“full tidal cycle”) was done in the field and tested the consequences of different setting times and levels of wave action on the survival of zygotes over a complete tidal cycle (approximately 12 h). In all experiments, we refer to “survival” as zygotes remaining attached to experimental surfaces. We note that young zygotes (up to a few hours old) may have the ability to re-attach but older zygotes probably cannot.

2.1. Study sites

All laboratory work was done in our experimental algal facility at the University of Canterbury Field Station in Kaikoura. The field site for the single-wave experiments was a sheltered reef (Lab Rocks) in front of the field station (42°25' S, 173°41' E; Fig. 1). The second set of experiments was done at two sites within each of three categories of wave exposure around the Kaikoura Peninsula. This area has sites of a wide range of exposures to wave action, from sheltered sites in the lee of headlands protected from oceanic swells, to very exposed sites continuously exposed to oceanic swells. The wave exposure

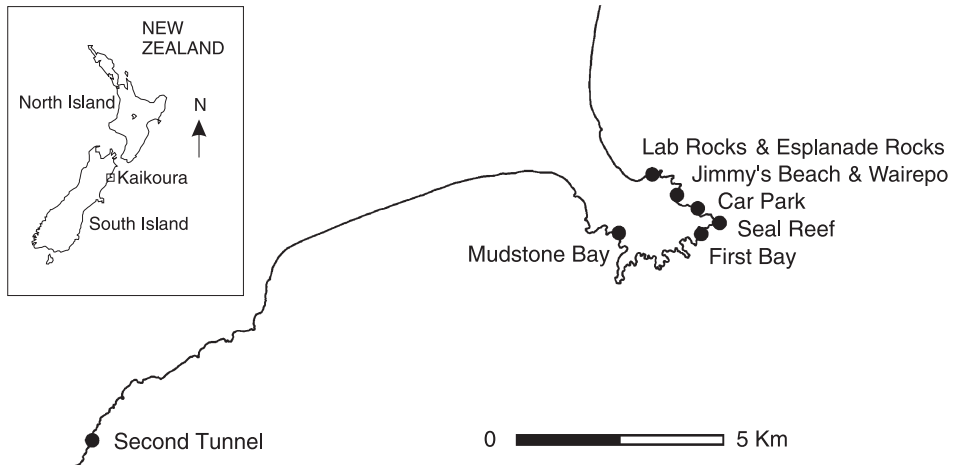


Fig. 1. Map of the South Island of New Zealand showing the Kaikoura peninsula and the sites used in the experiments.

categories were sheltered, intermediate and exposed. They were selected on the basis of other work we have done within these sites in which dynamometers were used (Bell and Denny, 1994) and on the predicted direction of swell for the 12 h of the experiment (Meteorological Service Report).

Within both sets of experiments, there were two runs, comparing species with different reproductive periods (see below). However, in the second set of experiments (those lasting 12 h), we were unable to use the same sites for both runs. This was because of a change in direction of the predicted swell and also a spill of 8 tonnes of rat poison that prevented access to some of the sites. For both sets of experiments, sheltered sites had a range of wave heights between 5 and 20 cm; intermediate sites had between 30 and 50 cm and exposed sites between 100 and 150 cm.

2.2. Species studied

We used different combinations of species in our experiments. This was dictated by the reproductive periodicity of the species. *D. antarctica* is a dioecious species that releases gametes naturally over a 16-week period during winter (May–August) (Hay, 1979b; Clayton, 1990). Raised male and female conceptacles scattered over the blades identify reproductive plants (Adams, 1994). *H. banksii* is a perennial, dioecious, fucalcan alga that dominates the middle to lower shore on many sheltered and intermediately exposed platforms. Populations release gametes throughout the year, but there are large pulses during the warmer months (September–April) (Schiel, unpublished data). *C. torulosa* is a perennial, monoecious, fucalcan alga that reproduces in pulses in spring and summer (September–January). All three species are fertilized externally, which seems to occur quickly after release (personal observation). There is no obligate planktonic developmental stage for these species.

During winter of 2000 and 2001 (for *D. antarctica* and *H. banksii* experiments), and spring and summer 1999/2000 (for *Hormosira* and *C. torulosa* experiments), reproductive male and female plants were collected in the field and returned to the laboratory where they were refrigerated at 4 °C for 24 h. Exposing plants to sunlight and warmth initiated gamete release. Gametes were washed from the adult plants using seawater, concentrated in glass beakers and left for 15 min to allow fertilization. The zygote suspension was then poured gently over plates covered with 1 cm of seawater. Approximately 100 plates per species were seeded for each experiment in large plastic trays at different time periods.

2.3. Experimental design

Fibre-based cement plates (trademark “Hardiflex”, James Hardy, used for exterior wall cladding) were used as a standard synthetic substratum for settlement. We have used these in numerous experiments and found them to have favorable water holding and attachment properties for fucalean algae. The surface of these plates is relatively smooth in appearance but at a microscopic level is covered with tiny pits and concavities, affording a heterogeneous surface for the small embryos. Plates were 7 mm thick and were cut into 5 × 5-cm squares. The plates were soaked in seawater for 24 h prior to settling with zygotes. We aimed for a settlement density of 500–1000 cm⁻², which is comparable to natural settlement densities (Schiel, unpublished data). Three settlement times were used. In all cases, plates were settled with zygotes 12, 6 and 1 h before beginning each experiment to represent the range of times within a full tidal cycle. Before and after each experiment, the number of zygotes on each plate was estimated by viewing the damp plate beneath a dissecting microscope and counting five random 1 cm² quadrats. Because we simultaneously tested different species and the three settlement times, large numbers of plates needed to be assessed for zygote numbers prior to each experiment. To manage this, three experienced people began counting zygotes on the plates at 11, 5.5 h and at 45 min for the different settlement times. Therefore, zygotes on all plates were counted in the hour before an experiment commenced and all plates were ready at the same time. Control plates for each species and settlement time were counted and treated exactly as experimental plates. During this process, no individual plate was out of water for more than a few minutes. Percent survival was calculated as the average number of zygotes remaining attached on each plate after an experiment.

The first set of experiments (single wave) tested the relative ability of zygotes of the three species to remain attached after different post-settlement times when exposed to an artificial standard wave in the laboratory and a single natural wave in the field. The single-wave experiment was done twice, once using *Hormosira* and *Cystophora* in summer 1999/2000 and once using *Hormosira* and *Durvillaea* in winter 2000. The artificial standard wave was created in the lab using a 20-l wave bucket (design described in Vadas et al., 1990) attached to the end of a glass-lined flume, which was 60 cm wide and 2 m long. By tipping the bucket, a wave about 5 cm high washed along the flume. For each run of the experiment, three replicate plates of each species from each post-settlement time period (1, 6, or 12 h) were positioned randomly in the centre of the flume and then exposed to a standard wave. There were three such runs (so, $n=9$ for each species at each settlement time). The lab experiments were done within 15 min and were initiated within 5 min of the

12-, 6- and 1-h settlement times. After each run, plates were returned to culture tanks. Immediately after the lab experiments, another set of plates of each species from each settlement period was taken to the field site across the road from the lab (Lab Rocks; transport time < 1 min) and exposed to one natural low-energy (ca. 5–10 cm) wave. To standardize their exposure, the plates were randomly positioned on a slotted plywood board that held them in place (as for Vadas et al., 1990). The board was then held against the shore and one low-energy wave was allowed to wash over it. Control plates were similarly handled and taken to the site. The field process took about 20 min. All plates were then returned to culture tanks and re-counted for remaining zygotes.

The second set of experiments done over a 12-h tidal cycle, tested survival after different setting times over three exposure levels, using two species. During summer 2000/2001 for *H. banksii* and autumn 2001 for *D. antarctica*, plates were settled with zygotes for each of three periods (1, 6 and 12 h), as in the first set of experiments. Two low-shore sites within three levels of wave action around Kaikoura Peninsula were used (Fig. 1). The plates were taken to field sites, attached in random positions in the lower mid-intertidal zone and left for 12 h before being retrieved. We were interested only in the wave climates of sites over the 12 h of each experiment; we standardized sites as much as possible by placing plates on platforms away from grazers and algal canopies. The number of zygotes on each plate was counted before and after placement in the field (as above). After the plates were counted, they were kept for a further 24 h in seawater to assess viability of zygotes. For *H. banksii*, the sheltered sites were at Lab rocks and Mudstone Bay, the intermediate sites were at Car Park and Jimmy's Beach and the exposed sites were at Second Tunnel and First Bay. For *D. antarctica*, sheltered sites were at Wairepo Beach and Mudstone Bay, intermediate sites were at Car Park and Esplanade Rocks, and exposed sites were at Seal Reef and First Bay. In all cases, zygotes were exposed to experimental treatments within about 20 min of their designated settling times of 1, 6 and 12 h. Control plates ($n = 3$ for each species at each settlement time) were taken to field sites and returned to culture at the start of each experiment.

Data were tested for homogeneity of variances using Cochran's test prior to Anova and were transformed when necessary. In all cases, these tests were nonsignificant unless otherwise stated. In some cases (see Results), the variances could not be homogenised,

Table 1

Two-factor analysis of variance of the effects of post-settlement attachment time (1, 6 or 12 h) and species on the percent survival of *H. banksii* and *C. torulosa* after a single wave in the laboratory (A) and in the field (B)

Location	Source	df	MS	F	P
(A) Laboratory	Settling time	2	22648.39	70.09	0.001
	Species	1	718.26	2.22	0.143
	Settling time × Species	2	60.19	0.19	0.831
	Residual	48	323.13		
(B) Field	Settling time	2	12218.79	36.95	0.001
	Species	1	1822.26	5.51	0.023
	Settling time × Species	2	6155.46	18.61	0.001
	Residual	48	330.73		

Cochran's tests were not significant.

which can affect interpretation of results (cf., Underwood, 1997). Analyses were done using Statistica 5.0 (Statsoft).

3. Results

In all experiments, control plates had 100% survival of zygotes, so no graphs or other analyses of these will be presented.

3.1. Single-wave experiments

In the single-wave experiment using *H. banksii* and *C. torulosa*, the duration of the post-settlement period had a significant effect on the survival of zygotes of both species when exposed to a single low-energy wave in the laboratory and in the field (Table 1A, B). The species had similar survival within each post-settlement category in the laboratory.

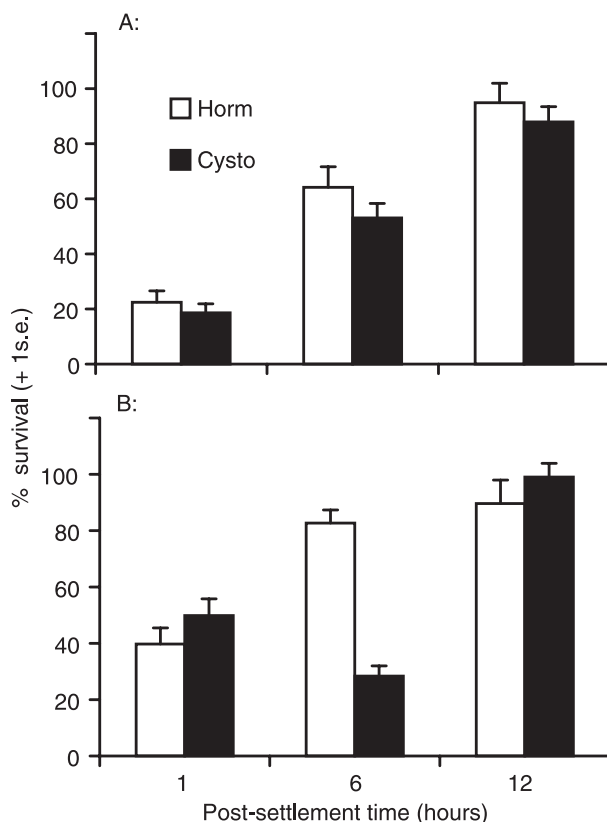


Fig. 2. The average percent survival (i.e. percentage of original numbers remaining attached) of *Hormosira* and *Cystophora* after exposure to a single wave in the Laboratory (A) and in the Field (B) after 1-, 6- or 12-h post-settlement attachment time.

When given 1 h to attach, only an average of 18–21% of *Cystophora* and *Hormosira* zygotes remained attached (Fig. 2A). After a post-settlement time of 6 h, survival improved to an average of 45–65%, and after 12 h to 85–95%.

The result was more complicated in the plates exposed to a single wave in the field. There was a significant interaction between species and post-settlement time (Table 1B) because of the relatively poor survival of *Cystophora* at 6 h (Fig. 2B). In the 1- and 12-h treatments, *Cystophora* averaged about 10% greater survival than *Hormosira*. *Hormosira* averaged 40%, 85% and 91% survival after 1, 6 and 12 h of post-settlement time. During the same post-settlement periods, *Cystophora* averaged 51%, 26% and 99% survival. The poor survival of *Cystophora* at 6 h is an unexplained anomaly. Both species tended to have greater survival in the field than in the laboratory.

In the single-wave experiment using *D. antarctica* and *H. banksii*, there were significant differences in survival between the species and post-settlement times in the laboratory flume (Table 2A). For all post-settlement attachment times, *Durvillaea* survived better than *Hormosira* (Fig. 3A); *Durvillaea* zygotes had 75%, 98% and 99.5% survival at 1-, 6- and 12-h post-settlement times, while the survival values for *Hormosira* were 2%, 18% and 44%. Although the survival of *Hormosira* zygotes increased as the post-settlement attachment period increased, the survival of zygotes at each post-settlement time was poorer in this experiment than in the earlier comparison with *Cystophora* in the laboratory flume (cf., Fig. 2).

Once again, the result was more complicated in the plates exposed to a single wave in the field. There was a significant interaction between species and post-settlement time (Table 2B), which was attributable to the similarity in survival of *Hormosira* zygotes in the 6- and 12-h treatments. As in the laboratory experiment, *Durvillaea* zygotes had much greater survival than *Hormosira* at all post-settlement times. *Durvillaea* survival average 92% after a 1-h attachment time, but was almost 100% at 6 and 12 h (Fig. 3B). As in the laboratory experiment, *Hormosira* had only a few percent of zygotes survive after 1 h of attachment but this increased to 61–65% at 6 and 12 h.

The poorer survival of *Hormosira* during the experiment with *Durvillaea* compared to the experiment with *Cystophora* may be attributable to the experiment being done in

Table 2

Two-factor analysis of variance of the effects of post-settlement attachment time (1, 6 or 12 h) and species on the percent survival of *D. antarctica* and *H. banksii* after a single standard wave in the laboratory (A) and in the field (B)

Location	Source	df	MS	F	P
(A) Laboratory	Settling Time	2	5454.46	21.06	0.001
	Species	1	66108.99	255.26	0.001
	Settling time × Species	2	745.60	2.88	0.066
	Residual	48	258.98		
(B) Field	Settling Time	2	6958.23	27.76	0.001
	Species	1	34866.75	139.11	0.001
	Settling time × Species	2	4082.58	16.29	0.001
	Residual	48	250.64		

Variances could not be homogenized and Cochran's tests were significant.

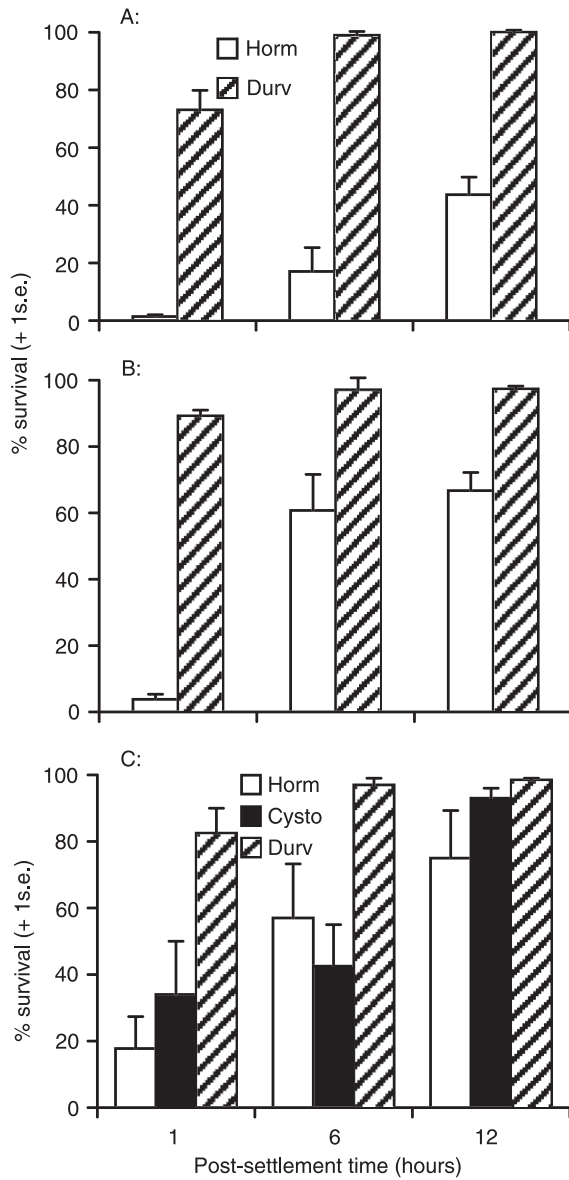


Fig. 3. The average percent survival of *Durvillaea* and *Hormosira* after exposure to a single wave in the Laboratory (A), in the Field (B) and in all single wave experiments (C) after 1-, 6- or 12-h post-settlement attachment time.

winter. This is probably not the optimal reproductive season of *Hormosira* and it may have affected zygote viability or attachment properties. However, all zygotes that survived and remained attached on plates had elongated 24 h after the experiments, indicating that they

were viable. Over the single-wave experiments, there was generally a progression of survival from sheltered to exposed species and from 1 to 12 h of attachment time (Fig. 3C). *Hormosira*, the species most characteristic of sheltered shores, had generally poorer survival than *Cystophora* (found in slightly more exposed situations), which was poorer than *Durvillaea* (found only in exposed conditions). *Durvillaea* clearly exhibited greater ‘stickability’ than the other species at all attachment times.

3.2. Full tidal cycle field experiments

When placed into the field for 12 h at sites within three levels of wave exposure, *H. banksii* zygotes had greatly different survival among the three post-settlement treatments, but this effect varied between sites within exposures (Table 3A). In all cases, there was far greater survival in the treatments with a 12-h period of attachment than those attached for 1 or 6 h (Fig. 4A). *Hormosira* zygotes settled for only 1 h had no greater than a few percent survival in any of the treatments, while those settled for 6 h averaged no more than 8% survival. Of the plates settled for 12 h, the greatest survival (40%) occurred in one sheltered site, while the other site within the same exposure had 22% survival. At the intermediate exposure, survival averaged 22% and 18%, while at the exposed sites, the averages were 65 and 8%. For *Hormosira* overall, therefore, there was very poor survival in exposed conditions and only those zygotes with >6 h of attachment time remained attached in any numbers after a full tidal cycle.

The survival of *D. antarctica* zygotes after 12 h in field sites did not depend on the post-settlement period but sites within exposures did vary (Table 3B). In most sites within the three levels of exposure, the average survival ranged from 83% to 99.5% (Fig. 4B). The exception was at one of the sites at intermediate exposure, where average survival ranged from 45% to 53%. This site was apparently hit obliquely with some freak waves, but the effect was similar among treatments with different post-settlement times. As in the

Table 3

Three-factor mixed model analysis of variance of the effects of exposure (sheltered, intermediate and exposed), sites (random and nested in exposure) and post-settlement attachment time (1, 6, or 12 h) on the percent survival of (A) *H. banksii* and (B) *D. antarctica* after 12 h in the field

Species	Source	df	MS	F	P
(A) <i>Hormosira</i>	Exposure	2	417.58	7.03	0.074
	Sites (Exposure)	3	59.36	1.94	0.141
	Settling time	2	1483.26	15.02	0.005
	Exposure × Settling time	4	252.75	2.56	0.146
	Sites (Exposure) × Settling time	6	98.78	3.22	0.012
	Residual	36	30.66		
(B) <i>Durvillaea</i>	Exposure	2	5423.20	2.12	0.267
	Sites (Exposure)	3	2563.36	11.29	0.001
	Settling time	2	48.68	0.56	0.600
	Exposure × Settling time	4	110.68	1.27	0.379
	Sites (Exposure) × Settling time	6	87.45	0.39	0.884
	Residual	36	227.128		

Variances could not be homogenized and Cochran's tests were significant.

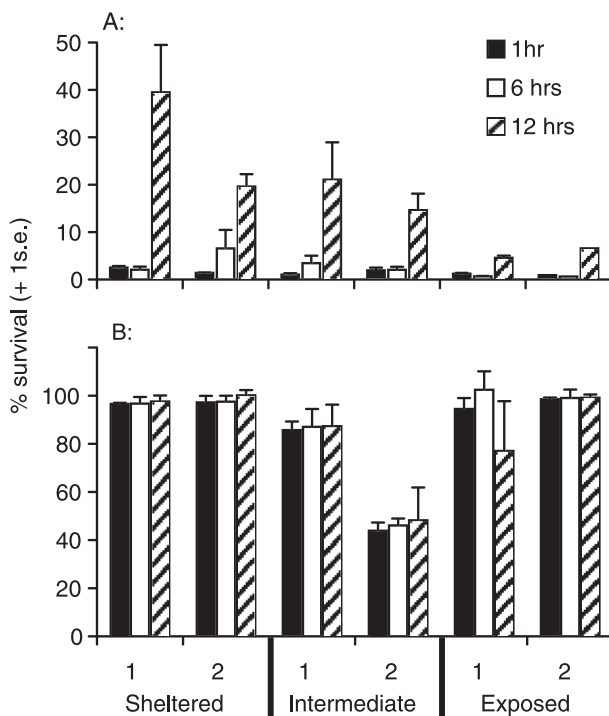


Fig. 4. The average percent survival of *Hormosira* (A) and *Durvillaea* (B) at sites within three exposures after one tidal cycle and 1-, 6-, or 12-h post-settlement attachment time.

earlier experiments, therefore, *Durvillaea* zygotes attached quickly and firmly, surviving even after 12 h in exposed sites subjected to 1.5-m swells.

4. Discussion

Life in the turbulent environment of the intertidal zone on temperate shores presents many challenges to resident organisms. Several reviews have discussed the factors affecting the various stages of development of algal stands including gamete release, fertilization, the dispersal period, settlement, attachment, recruitment and subsequent growth (Chapman, 1985; Santelices, 1990; Clayton, 1992; Fletcher and Callow, 1992; Vadas et al., 1992). The early post-settlement period involves the interaction of microscopic zygotes, embryos and germlings with many physical and biological factors (Amsler et al., 1992). Vadas et al. (1992) list 6 intrinsic factors and 17 extrinsic factors that can influence early post-settlement mortality. Intrinsic factors include properties of species such as germination and spore viability, attachment time, and growth rates and size. Extrinsic factors include interactions with other species, substratum characteristics and physical environment effects such as temperature and water motion. It has long been recognized, however, that secure attachment is one of the most important events in the life

history of intertidal algae (Hardy and Moss, 1979). Our study focused primarily on water motion and how its effects on the survival of early post-settlement stages varied among three of the most important habitat-forming seaweeds in southern New Zealand. These species have overlapping distributions geographically but not locally. *H. banksii* and *C. torulosa* are both widely distributed species found throughout coastal New Zealand and the offshore islands (Nelson, 1994). Within sites, however, *C. torulosa* is a low-shore species that readily desiccates and dies if emersed for too long. *H. banksii* has a narrow zone of overlap with *C. torulosa* but mostly occurs higher in the intertidal zone and is the most desiccation-resistant of the New Zealand large brown algae (Brown, 1987; Chapman, 1965). Both species are found in sheltered and intermediate conditions of wave exposure and rarely extend into exposed conditions except as isolated and stunted individuals. *D. antarctica* is found only in exposed conditions and is one of the largest of all intertidal species along parts of the open coast of New Zealand, South America and most of the sub-antarctic islands (Batham, 1956; Hay, 1979a,b; Nelson, 1994). On a local scale, it never extends into sheltered or intermediate conditions.

Our results indicate that the ability to remain attached immediately after settlement represents a major bottleneck in the establishment of at least two of these species across wave exposures. Attachment ability broadly correlated with the natural distribution of these species across a wave exposure gradient with overall rankings of average survival of *Durvillaea*>*Cystophora*>*Hormosira*. Furthermore, both *Hormosira* and *Cystophora* required at least 6 h to adhere to surfaces, even in sheltered conditions, while *Durvillaea* adhered well and quickly in all experimental conditions. It is a tautology to say that these species are well adapted in their early stages to the environment in which they normally occur. However, there are clear and important differences in the propagules of each species.

Most algal propagules sink slowly through water, which is a viscous medium to objects only 50–100 µm in diameter (Amsler et al., 1992; Norton, 1992). Both *Cystophora* and *Hormosira* have relatively large eggs (60–120 µm) that separate quickly after release from parents and sink slowly. *D. antarctica*, however, releases very small propagules (30 µm) in packets of four that are relatively buoyant, probably because of small size and the copious amounts of mucilage released simultaneously (Clayton, 1992), and can remain suspended for up to 15 min in calm test-tube conditions (Taylor, unpublished data). The differences among species in size and buoyancy clearly signal that their pre-settlement processes and adaptations are likely to be quite different.

Gamete release in *H. banksii* and *C. torulosa* occurs at low tide in calm conditions, although it is not known if this is exclusively so. This is typical of fucalean species. For example, gamete release in *Fucus distichus* occurs during low tides in periods of very low water motion (Pearson and Brawley, 1996). High water motion can inhibit gamete release in *F. vesiculosus*, *F. distichus* and *Pelvetia fastigiata* and result in low fertilization success (Serrao et al., 1996). The timing of propagule release is probably crucial to survival. We have seen *Hormosira* and *Cystophora* release eggs into tidal cracks and pools within an hour of low tide, which would allow up to several h for attachment to the substratum to occur. The processes following gamete release in *Hormosira* and *C. torulosa* are similar to most fucaleans (Fletcher and Callow, 1992; Clayton, 1992; Vreeland et al., 1993). Two or three hours after fertilization, *Hormosira* zygotes become sticky from extracellular

mucilage and adhere to the substratum (Forbes and Hallam, 1979). At 5 h, a gentle jet of water will not dislodge them and at 8 h they appear to be firmly attached. Not until 16 h after fertilization have 50% of zygotes developed rhizoids. In other species of fucalans, there are two periods of greater mortality at these very early post-settlement stages. The first is immediately after settlement, before sufficient mucilage is produced for adhesion, and the second is just after the rhizoids have formed and the mucilage attachment weakens at 24–48 h (Brawley and Johnson, 1991). Our experiments extended only through the period of attachment by mucilage. For both *Hormosira* and *C. torulosa*, the attachment was strongest at 12 h, a period that exceeds the emersion time at low tide. Across exposures, *Hormosira* had no more than 8% survival and this was only at the calmest sites. The better adhesion at 12 h after settlement strongly implies that successful attachment is likely to occur only in the calmest conditions, which rarely, if ever, take place at exposed sites. However, the occasional presence of a stunted form of *Hormosira* on exposed shores indicates that there may be “windows” of suitable conditions for successful settlement in more turbulent environments. Based on our results, these are most likely to occur during occasional periods of very calm sea conditions, when wave action and tidal flows are reduced, and most likely during spring when desiccation at low tide is unlikely to be as intense as in summer.

In contrast, *D. antarctica* zygotes attach immediately and firmly to almost any surface. Even wiping a gamete-releasing frond over a surface results in extensive attachment of zygotes by a sticky mucilage. In all of our experiments, adhesion of zygotes was almost 100% in most cases and did not depend on the degree of exposure to water motion. The processes and timing of gamete release, dispersal ability and settlement are not clear in this species. Adult plants occur in the low-shore at the subtidal boundary and are rarely exposed entirely except during the lowest tides. We have seen release occur at low tide in calm conditions but do not know if this is exclusively so. We hypothesize two processes of attachment. Because oogonia are released in packets of four within copious quantities of dense mucilage, they probably remain near the surface and are propelled quickly shorewards at low tide where they are likely to contact substrata near adult plants. The other means of short-range dispersal is by gamete-releasing fronds coming into direct contact with the shore. We have seen “smears” of *Durvillaea* gamete-bearing mucilage on bare rock at low tide, but do not know how frequent an occurrence this is. However, because propagules of *Durvillaea* are relatively buoyant, this species clearly has a potential mechanism for medium to long-range dispersal of propagules in comparison to other intertidal furoid algae. Even though the non-floating propagules of intertidal furoids are likely to be suspended in the turbulence of water motion nearshore for short periods (Norton, 1992), they do not seem to be able to attach quickly and securely, and therefore they probably have little ability to disperse effectively as propagules. For *D. antarctica*, however, the ability of propagules to adhere quickly and securely may make relatively long-range dispersal effective. The inshore area around southern New Zealand reefs can be strongly influenced by along-shore transport (Chiswell and Schiel, 2001), which provides a potential avenue of dispersal along the coast.

Many factors affect the viability of settled algal propagules. Substratum characteristics such as surface heterogeneity, texture of microsites and ability to retain water can affect early survival (Harlin and Lindbergh, 1977; Hardy and Moss, 1979; Brawley and Johnson,

1991, 1993). One problem in assessing processes across different wave climates is that rock types can vary considerably across sites of different levels of exposure. Softer sedimentary rock types such as sandstone and siltstone often support very different algal communities to harder metamorphic and volcanic rock surfaces such as marble and basalt (Stephenson, 1961; Hartog, 1972; Fletcher and Callow, 1992). In southern New Zealand, intertidal platforms at exposed sites are often composed of harder volcanic rock while reefs at many sheltered sites are composed of softer rock types like mudstone and sand stone. Rock type was not a factor in our experiments because we used standard plates, which we know to be good surfaces for algae to survive and grow on across exposures. Although the role of rock type in determining algal community development is largely unknown, it could be an important factor in the failure of large species such as *D. antarctica* to extend into more sheltered shores, even if they successfully settled there.

As the size of developing plants increases, the forces exerted by waves may exceed the strength of attachment (Vogel, 1984; Denny, 1995). This may not necessarily be due to the attachment strength of the holdfast to the substratum but because the substratum itself fractures so easily. For example, it is not uncommon to see limpets detached and cast up on the beach still firmly attached to a piece of a fractured rock. Our experiments clearly highlight the differences between species in their initial post-settlement period. The lack of intrusion of the more sheltered species, *H. banksii* and *C. torulosa*, into exposed situations is greatly influenced by their inability to attach securely. Because there are no reproductive stands of these species in exposed areas, whatever gamete arrival, attachment and settlement that occurs is likely to be in low numbers. This may affect fertilization success (e.g. Denny and Shibata, 1989; Reed, 1990b; Serrao et al., 1996; Brawley et al., 1999) and potentially other factors that are density dependent. Low-density settlement may also provide too few numbers to survive other processes such as grazing, competition and desiccation (Reed, 1990a,b; Vadas et al., 1992; Worm and Chapman, 1996, 1998).

The viability of settled zygotes may also be different among species and across environmental gradients. For the species we examined, there appear to be narrow windows through the bottleneck for securing a place on a reef. *H. banksii* and *C. torulosa* need extended calm periods to attach successfully but these must also coincide with times when they will not desiccate (cf. Brawley and Johnson, 1993; Underwood, 1998). For *D. antarctica*, the reproductive period is relatively brief and occurs during the stormy winter months when turbulent conditions prevail. Although it is capable of remaining attached in all conditions, its absence from more sheltered areas suggests that other processes are determining its distribution. For example, over a short-time scale, fertilized zygotes may simply not arrive in sufficient numbers to establish on shores outside its adult range (Clayton, 1990; Reed et al., 2000). The demographics of these early stages are clearly of great ecological importance to the development of habitat-forming algal stands, intertidal habitats and subsequent community processes.

Acknowledgements

Thanks to G. Thompson and R. Dunmore for the assistance in the field and the University of Canterbury for logistical support. Also, thanks to Dan Reed for his time and

helpful comments that improved this manuscript. We thank two anonymous referees who made many valuable suggestions. This work was funded by a University of Canterbury/N.I.W.A. Centre of Excellence in Aquaculture and Marine Ecology scholarship, an Andrew Mellon Foundation Scholarship and by the Foundation of Research, Science and Technology, Grant Numbers UOC 412 and 610. We thank all of these for their continued support. [AU]

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