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Short communication

Recruitment and colonisation of vegetative fragments of *Posidonia australis* and *Posidonia coriacea*

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Abstract

Vegetative fragment recruitment of both *Posidonia australis* and *Posidonia coriacea* was observed on Success Bank, Western Australia, beginning in November 1993 ($n = 106$). Recruitment of vegetative fragments was defined as attachment to the substrate and subsequent rhizome extension. Rhizome extension occurred in 31% of all recruited *P. australis* vegetative fragments, yet no extension was detected in recruited *P. coriacea* vegetative fragments. In shallow water (<9 m), *P. australis* vegetative fragment recruits extended at an average rate of 0.78 ± 0.02 mm per day, but did not survive for more than 10 months. This extension rate was slightly less than in situ meadow rhizomes of established *P. australis* plants (1.01 ± 0.19 mm per day) from the same depth. The majority (78%) of deep water (10–12 m) *P. australis* vegetative fragment recruits survived >10 months, with rhizomes extending at slower rates (0.41 ± 0.02 mm per day) than shallow water recruits. No in situ seagrasses grew at the deep site for direct comparison.

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1. Introduction

Seagrass communities are an integral component of marine ecosystems that experience cyclical succession, often reset by disturbance. Seagrass meadow structure and maintenance can typically be explained using patch dynamics (McRoy and Lloyd, 1981; White and

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Pickett, 1985; Duarte and Sand-Jensen, 1990; Marba and Duarte, 1995; Vidondo et al., 1997; Kendrick et al., 1999).

When a disturbance occurs, the rate and pattern of recruitment into the “new” patch is directly related to species-specific availability of propagules at the time of disturbance (Denslow, 1985). Species with seed banks (e.g. *Zostera marina*) are at a distinct advantage, being capable of rapid recruitment into a disturbed patch if conditions are right, regardless of the timing of sexual production. Species that lack a seed bank (e.g. *Posidonia australis*) are at a disadvantage given that the availability of sexual propagules will be limited to the period (season) and duration of reproduction. One method these species may utilise to surmount this disadvantage is the ability for vegetative fragments to act as dispersal recruitment units. This method is improbable for *Z. marina* (Ewanchuk and Williams, 1996) and vegetative recruitment has yet to be documented for any ‘climax’ seagrass species, such as *P. australis* and *Posidonia coriacea* (Kendrick et al., 1999). In contrast, there is evidence that many pioneer species utilise asexual propagation, via fragmentation as a dispersal mechanism (McConchie and Knox, 1989).

This paper focuses on two Australian species, *P. australis* and *P. coriacea*. No vegetative recruitment (via rhizome fragments) of *Posidonia* species has been quantifiably reported in Australia. Gordon et al. (1996) postulated that large “clumps” of meadow might slip down newly dredged slopes (retaining an intact patch), yet they provided no empirical evidence. To date there is a lack of data quantifying the regrowth abilities of vegetative fragments and their establishment (colonisation) potential.

This paper presents evidence of vegetative fragment recruitment, colonisation, and survival of a climax species, in Western Australia. This evidence can thus be used to illustrate that vegetative fragment recruitment may be a contributing component to patch colonisation and meadow expansion in *Posidonia* seagrasses on Success Bank, Western Australia. The hypothesis being tested is: vegetative fragments of *Posidonia* species recruit to and colonise new areas.

2. Materials and methods

2.1. Site

A transect (hereafter recruitment transect) was established on Success Bank (32°05'94"S, 115°43'23"E), Western Australia. Five sites (each site approximately 0.2 ha) were established along this transect down a depth gradient from 4.9 (site 1) to 12.0 m (site 5). Sites 1–3 are referred to as shallow water sites (<9 m), with sites 4 and 5 being referred to as deep water sites (10–12 m) in this study. Site 1 had an established mixed seagrass meadow assemblage, seagrass was patchy at site 2 (including *P. australis* and *P. coriacea*) and site 3 (ephemeral species only), and sites 4 through 5 had no seagrass.

Irradiance on the recruitment transect ranged from 321 ± 92 at 5 m depth to $112 \pm 17 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 12 m depth, during summer (Campbell, 2000). During winter, irradiance ranged from 144 ± 42 at 5 m depth to $88 \pm 11 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 12 m (Campbell, 2000).

2.2. Measuring rhizome extension

Rhizome extension was measured in situ by tagging meristems with a small plastic “cable tie” marking the last shoot on the rhizome prior to the apical meristem (similar to the methods of [Caye and Meinesz, 1985](#)). Rhizome extension beyond the tagged area was used as an indication of growth while reduction in rhizome length was used as an indication of necrosis.

2.3. In situ meadow rhizome extension

For comparative purposes, 60 *P. australis* and 20 *P. coriacea* in situ meadow rhizomes were tagged and measured for extension, approximately three times a month, for 23 months. This occurred at the shallow water sites where seagrasses were abundant. No in situ meadow, or clumps of plants existed at the deep water sites.

2.4. Vegetative fragment recruitment

Natural vegetative fragment recruitment was observed and measured at each of the five sites on the recruitment transect. Vegetative fragment recruitment was considered to have occurred when a piece of unattached rhizome (e.g. storm debris) settled on the substrate and anchored (plants took root). Colonisation was defined as the recruit persisting (remaining in place for at least 2 months), producing roots and exhibiting rhizome extension. Definitions for recruitment and colonisation were defined *a priori* based on field and mesocosm studies ([Campbell, 2000](#)). Thus, both colonisation and mortality could be observed. Between each site, parallel to the transect, two transect lines of approximately 20 m length and 2 m wide were monitored for new rhizome recruits. New recruits lacked a cotyledon. When a new recruit was found, the apical meristem, or final node on a vegetative segment, was tagged and subsequent growth increments were measured approximately three times a month for 23 months. Sizes of recruited fragments were measured as the number of shoots present, and the presence or absence of flowering was recorded.

Vegetative fragments at sites 3–5 were readily identified as unattached rhizome recruits because no established *Posidonia* species were present at these sites, and seedling recruitment was not occurring when the vegetative fragments initially recruited. At shallow water sites *Posidonia* vegetative fragments were tagged and measured only when they settled in bare sand areas (such as meadow gaps and blowouts), thus providing incontrovertible evidence that the recruits were “new” fragments and unattached to meadows prior to tagging and measuring. Species were differentiated based on morphological characteristics.

2.5. Seedling recruitment

It was anticipated that seedling recruitment would be observed at this site. If this occurred in situ, *P. australis* seedling densities would be measured using 10 randomly placed 25 cm × 25 cm quadrats at each site. This would provide an average seedling density that could be extrapolated to average density per m². Seedlings would be determined by the presence of a cotyledon.

3. Results

3.1. *In situ* meadow rhizome extension

In shallow water, established *P. australis* rhizomes extended at an average rate of 1.0 ± 0.19 mm per day (site 1 = 1.04 ± 0.15 , site 2 = 0.96 ± 0.12 mm per day). *P. coriacea* rhizomes extended more slowly with an average rate of 0.48 ± 0.07 mm per day (site 1 = 0.49 ± 0.06 and site 2 = 0.46 ± 0.04 mm per day).

3.2. Recruited vegetative fragments

A total of 106 of *P. australis* and *P. coriacea* vegetative fragment recruits were identified at all sites on the recruitment transect (Fig. 1) during the sampling period. Thirty-one percent of the *P. australis* vegetative fragment rhizomes extended. All recruitment occurred after late spring/early summer (November, December and January) and late autumn (May and June) storms (Table 1). Six recruitment events were noted for *P. australis*, with November having the greatest recruitment in both 1993 and 1994. Only two recruitments events were noted for *P. coriacea* in November 1993 and May 1994. At a gross scale, the average annual recruitment rate was 55 vegetative fragment recruits ha^{-1} per year, with a maximum of 23 vegetative fragment recruits ha^{-1} in a single month at a single site. Extension did not occur in any *P. coriacea* fragments, yet it occurred in *P. australis* fragments. Survival times for vegetative fragments varied with depth (Table 2), however insufficient numbers and temporal variation prevented analysis of depletion curves as a function of depth.

Significantly more vegetative fragments of *P. australis* recruited ($F_{[1,8]} = 9.15$, $P < 0.05$; Fig. 1). As depth increased the number of recruited *P. australis* fragments increased linearly, whereas the opposite was true for recruits of *P. coriacea* ($r^2 = 0.8025$; $r^2 = 0.5326$, respectively; Fig. 1). The size of recruited fragments ranged from 10 to 46 shoots per individual, averaging 28.4 ± 1.09 shoots per individual. There was no trend between vegetative fragment size and recruitment depth ($F_{[1,103]} < 0.001$, $P > 0.05$). All vegetative fragment recruits observed survived for more than 2 months. Flowering was not observed.

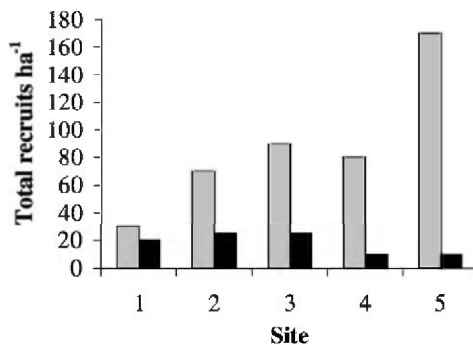


Fig. 1. The total number of recruited *P. australis* and *P. coriacea* vegetative fragments (extrapolated to no. ha^{-1}) over the duration of the study (23 months) at sites 1–5 on Success Bank, Western Australia. Depth increases between sites 1 (5 m) to 5 (12 m). (□) denotes *P. australis* and (■) denotes *P. coriacea*.

Table 1

Recruitment periods for *P. australis* and *P. coriacea* vegetative fragments (extrapolated to no. recruits ha⁻¹) at each 0.2 ha site

Month	Site	Depth (m)	Total recruits (no. ha ⁻¹)	
			<i>P. australis</i>	<i>P. coriacea</i>
November 1993	1	4.9	20	20
	2	5.8	40	10
	3	8.6	50	10
	4	10.7	45	10
	5	12.0	115	10
December 1993	2	5.8	5	0
	3	8.6	5	0
	4	10.7	10	0
	5	12.0	5	0
January 1994	3	8.6	5	0
	4	10.7	5	0
	5	12.0	10	0
May 1994	1	4.9	10	0
	2	5.8	20	15
	3	8.6	5	15
	4	10.7	15	0
June 1994	3	8.6	5	0
November 1994	2	5.8	5	0
	3	8.6	20	0
	4	10.7	5	0
	5	12.0	40	0

At site 1, six *P. australis* and four *P. coriacea* vegetative fragments recruited and survived for approximately 10 months (average *P. australis* survival 8.7 ± 0.42 months and average *P. coriacea* 9.0 ± 0.0 months). Three *P. australis* fragments colonised, with an average rhizome extension rate of 0.78 ± 0.02 mm per day. Sites 2 and 3 recruited many more *P. australis* (14 and 18, respectively) and *P. coriacea* vegetative fragments (5 and 5, respectively), however none survived for more than 6 months and no rhizome extension was observed. Thus, in shallow water, only three fragments colonised, with an average rhizome extension rate for *P. australis* of 0.78 ± 0.02 mm per day.

At site 4, 16 *P. australis* and two *P. coriacea* vegetative fragment recruits were observed with none surviving for more than 4 months. Of these, two *P. australis* vegetative fragments colonised with rhizome extension rates averaging 0.56 ± 0.01 mm per day. At site 5, a total of 36 vegetative fragment recruits were observed (34 *P. australis* and two *P. coriacea*), of which 28 *P. australis* vegetative fragments colonised with rhizome extension averaging 0.40 ± 0.02 mm per day. *P. coriacea* recruited and survived for the entire study, yet no vegetative fragments exhibited rhizome extension. In total, 78% of the vegetative fragments at site 5 colonised, surviving for >2 months and exhibiting rhizome extension. Only 69% (for both species) survived the duration of the 23-month study. As depth increased, extension rates significantly decreased ($F_{[1,31]} = 28.5$, $P < 0.0001$). In addition, the recruited

Table 2

Survival duration (months) of *P. australis* and *P. coriacea* vegetative fragments (extrapolated to no. surviving recruits ha⁻¹) at each 0.2 ha site

Survival duration (month)	Site	Depth (m)	Number of surviving recruits (no. ha ⁻¹)	
			<i>P. australis</i>	<i>P. coriacea</i>
3	3	8.6	5	0
	4	10.7	70	10
4	2	5.8	5	0
	3	8.6	10	0
	4	10.7	10	0
5	2	5.8	65	25
	3	8.6	75	25
8	1	4.9	20	0
9	1	4.9	0	20
10	1	4.9	10	0
	5	12.0	40	0
21	5	12.0	10	0
22	5	12.0	10	0
23	5	12.0	115	10

vegetative fragment extension rates were significantly lower than established in situ meadow rhizomes ($H_{[40]} = 47.6$, $P < 0.05$).

3.3. Recruited seedlings

Recruitment of seedlings was not observed at the study site.

4. Discussion

4.1. In situ meadow rhizomes

P. australis meadow rhizomes extended at a rate of 1.0 ± 0.19 mm per day, which falls within reported rates in the literature (0.07–2.17 mm per day; Clarke and Kirkman, 1989; West, 1990; Kirkman, 1995; Paling and McComb, 2000). *P. coriacea* rhizomes extend at a slower rate of $\sim 0.48 \pm 0.07$ mm per day than *P. australis*. These rates are the first published for *P. coriacea* and are within Kendrick et al.'s (1999) projected rates of rhizome extension (0.27–1.37 mm per day) for their deterministic model of seagrass extension. This study demonstrates that 100% of tagged meadow rhizomes ($n = 80$; 60 *P. australis* and 20 *P. coriacea*) were actively growing, in contrast to West (1990), who reported that there were few (1 in 600) actively growing shoots present in a *Posidonia* meadow on the Australian east coast. As measured in Western Australia, established *P. australis* in situ meadow growth

is active and extension rates are sufficient for vegetative expansion, exceeding values for *Z. marina* (0.44 mm per day; Olesen and Sand-Jensen, 1994), which has been reported to spread rapidly.

4.2. Recruited vegetative fragments

The recruitment of vegetative fragments occurred at all depths, however both *P. australis* and *P. coriacea* vegetative fragment recruits experienced moderate to low colonisation success as defined herein. The large size (28.4 ± 1.09 shoots per individual) of the fragments and lack of a cotyledon confirms that they were pieces of dislodged meadow rhizome rather than seedlings.

The degree of recruitment, colonisation and survival varied at each site (Table 1). Recruitment of *P. australis* was more successful at depth (9–12 m; $F_{[1,8]} = 9.15$, $P < 0.05$), in terms of both numbers (Fig. 1 and Table 1) and survival (Table 2). Recruitment events at all sites and mortality at shallow sites appear to have been correlated with storm activity creating, transporting, and removing fragments.

Vegetative fragments that recruited to shallow water (<9 m) typically did not survive for more than 10 months (Table 2). Both local wind-generated (short amplitude) and storm-generated (long amplitude) waves create high-energy orbital currents that can penetrate to 10 m depth in this region (Paling et al., 2000). At sites 2–4 (depth range between 5 and 10 m) survival times were <6 months for both species. In contrast, vegetative fragments at site 1 survived for 8–10 months and appeared to have been removed only following large storm events. The presence of an extant seagrass meadow significantly reduces the impact of wave-associated disturbances (Fonseca and Cahalan, 1992; Reusch and Chapman, 1995; Worm and Reusch, 2000; Campbell and Paling, in press). Increased survival times at site 1 are likely associated with the extant seagrass meadow, which is absent at sites 2 through 5. Wave activity does not appear to impact vegetative fragment mortality in deep water (site 5, 12 m) as evidenced by long term survival of all recruits. The relationship between depletion (survival) rates and depth could not be calculated from this dataset, however could provide significant insight into the role of vegetative fragment recruitment in the establishment and maintenance of seagrass beds.

During the 23 months of this study, no recruitment of *Posidonia* seedlings was observed. Although at close-by (within 5 nm) sites, recruitment of *Posidonia* seedlings was observed to occur (maximum of 39 seedlings m^{-2} per month; Campbell, 2000).

Extension rates were significantly slower in deep water (0.40 ± 0.02 mm per day) compared to shallow sites (0.78 ± 0.02 mm per day; $F_{[1,31]} = 28.5$, $P < 0.0001$). No *P. coriacea* vegetative fragments were seen to extend, which may be due to the rhizome growth pattern exhibited by this species.

Lack of growth in some fragments may have been due to the fragment rhizome length being too small. For example, in freshwater systems it is thought that aquatic plant fragments require a minimum length to regrow (Barrat-Segretain et al., 1998). The minimum required rhizome length for *Posidonia* species to regrow is unknown.

The extension rates in both the shallow (0.78 ± 0.02 mm per day) and deep water (0.40 ± 0.02 mm per day) vegetative recruits were within reported extension rates for in situ *P. australis* rhizomes 0.07–2.17 mm per day (see above). However, recruited vegetative

fragments in both shallow and deep water extended at a slower rate than in situ meadow rhizomes in this study. This may be a reflection of the damage that recruited vegetative fragments may have experienced (i.e. most vegetative fragments were storm debris), and with convalescence of damage to vegetative fragments over time, the extension rates may become similar to in situ meadows.

Extension rates of vegetative fragments significantly decreased with increasing depth. However, there is no indication that irradiance was the limiting factor at the depths examined on the recruitment transect during the study. At all depths irradiance exceeded reported onset of saturation irradiance (I_c) of *P. australis* from southern Western Australia ($25 \mu\text{mol m}^{-2} \text{s}^{-1}$, Masini et al., 1995). Irradiance remained above 25% surface irradiance ($102 \mu\text{mol m}^{-2} \text{s}^{-1}$) during summer, with irradiance at the deepest site (site 5) being equivalent to 27.5% surface irradiance.

Although irradiance is not limiting to healthy, established plants, vegetative fragment recruits may require higher irradiance levels, as suggested by a decrease in the rate of rhizome extension with depth. This is possibly due to damage vegetative fragments attain when separated from the meadow, or during dispersal before settling.

The most significant result from this work is the observation of successful colonisation (recruitment, persistence and growth) of vegetative fragments of *P. australis*. Typically species colonise a patch in three ways: (1) they laterally invade bare patches by propagation from the adjacent meadows; (2) they colonise bare areas randomly, regardless of proximity of nearby patches; and (3) use an intermediate recolonisation pattern. For example, *Z. capricorni* recolonises disturbed areas by propagation from adjacent meadows (Rasheed, 1999). The evidence from this study infers fragmentation of *Posidonia* rhizomes and dispersal by drift yields propagules that are neutrally buoyant, viable plants that can recruit and colonise in a random pattern, survive and grow.

Kendrick et al. (1999, 2000) have documented that seagrass meadows on Success Bank are expanding. Yet a discrepancy exists between the estimated and actual expansion of meadows and patches on Success Bank, which may be explained by the recruitment of vegetative fragments. As yet, there have been no studies to determine if recruitment of vegetative fragments is occurring on the east coast of Australia.

The deterministic model, developed by Kendrick et al. (1999) oversimplifies the patch dynamics of Success Bank. However, Kendrick et al. (1999) note that this can be improved upon by the addition of seedling recruitment, patch formation, survival and growth data. This study indicates that vegetative fragment recruitment may be a factor in the maintenance and expansion of *Posidonia* seagrass meadows and therefore should be considered for incorporation into the Kendrick et al. (1999) deterministic model.

In conclusion, this study provides empirical evidence that vegetative fragments recruit, colonise, and survive, supporting the hypothesis that in Western Australia, *Posidonia* species vegetative fragments can recruit to and colonise new areas.

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