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Aquatic Botany 74 (2002) 287–297

**Aquatic  
botany**

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## Interannual and small-scale spatial variability in sexual reproduction of the seagrasses *Posidonia coriacea* and *Heterozostera tasmanica*, southwestern Australia

Meredith L. Campey, Gary A. Kendrick, Diana I. Walker\*

Department of Botany, The University of Western Australia, Crawley, WA 6009, Australia

Received 6 July 2001; received in revised form 12 June 2002; accepted 12 July 2002

### Abstract

Sexual reproduction in *Posidonia coriacea* Kuo and Cambridge and *Heterozostera tasmanica* (Aschers.) Dandy on Success Bank, Western Australia, was assessed over a 3-year period (1996–1998). Interannual and spatial variation in inflorescence, flower and seed density and the probability of flowers setting seed were examined for both species of seagrass. Flower and seed densities of *P. coriacea* showed that sexual reproduction could contribute to the maintenance of this population on Success Bank. Substantial interannual variation in flowering intensity indicates that the relative contribution of sexual reproduction to meadow maintenance varies among years. Flower densities of *H. tasmanica* in 1997 pointed to potential sexual reproduction as a contribution to the meadow, but the absence of flowers in the 2 other years of the study, and the absence of a seed bank within the sediment, suggested that sexual reproduction did not contribute to the maintenance of this population on Success Bank. Seed production determines the upper bounds of the potential for a species to recruit. We have quantified these upper bounds for *P. coriacea* and *H. tasmanica* on Success Bank, southwestern Australia at  $15 \pm 3$  and  $60 \pm 11 \text{ m}^{-2}$  per year (mean  $\pm$  S.E.,  $n = 110$ ), respectively. These upper bounds are comparatively low relative to vegetative shoot recruitment at  $240 \pm 84$  and  $360 \pm 86 \text{ m}^{-2}$  per year (mean  $\pm$  S.E.,  $n = 6$ ) for *P. coriacea* and *H. tasmanica*, respectively.

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**Keywords:** *Posidonia coriacea*; *Heterozostera tasmanica*; Sexual reproduction; Flowers; Seeds; Success Bank; Australia

\* Corresponding author. Present address: School of Plant Biology, Faculty of Nature and Agricultural Sciences, 35 Stirling Highway, WA 6009, Crawley, Australia. Tel.: +61-8-9380-2089; fax: +61-8-9380-1001.

E-mail address: diwalker@cyllene.uwa.edu.au (D.I. Walker).

## 1. Introduction

The maintenance of seagrass meadows was once thought to occur predominantly through asexual clonal growth, as flowers and seedlings were observed infrequently (McMillan and Moseley, 1967; Den Hartog, 1970; Tomlinson, 1974; Orth, 1976). More recent studies, examining flowering in seagrasses, have found widespread and frequent sexual reproduction in many species (e.g. *Zostera marina*: Phillips et al., 1983; *Thalassia testudinum*: Durako and Moffler, 1987; *Cymodocea nodosa* and *Zostera noltii*: Buia and Mazzella, 1991; *Cymodocea nodosa*: Terrados, 1993; *Halodule wrightii*: Ferguson et al., 1993; *Phyllospadix torreyi*: Williams, 1995; *Zostera capricorni*: Peterken and Conacher, 1997; *Posidonia australis*: Waycott et al., 1997). Reported seagrass reproduction is patchy across scales of tens of meters and varies greatly among years (Larkum, 1976; West and Larkum, 1979; Buia and Mazzella, 1991; Inglis and Lincoln Smith, 1998). The goal of this paper is to assess the small-scale spatial distribution and the interannual variation in flowering in two co-occurring seagrass species, *Posidonia coriacea* and *Heterozostera tasmanica*, in a 1.1 ha area on Success Bank, Western Australia.

*Posidonia coriacea* and *Heterozostera tasmanica* occur in mixed species meadows on Success Bank, which is a wave-exposed shallow (<10 m) coastal sand bank (Kendrick et al., 2000) near Perth, Western Australia. *Posidonia coriacea* has increased in cover by 140 ha over the past 30 years (1965–1995; Kendrick et al., 2000). Modeling of growth based solely on rhizome spread (Kendrick et al., 1999) does not account for this increase, and suggests that recruitment from seedlings is contributing to increases of seagrass coverage in this location. This study examines the role of flowering and seed set in *Posidonia coriacea* and *Heterozostera tasmanica* at a location on Success Bank to assess the maximum potential for recruitment from seeds for these seagrass species. Inglis (2000a), in his review of variation in seed production, dispersal and recruitment strategies of seagrass genera, regarded *Posidonia* as being capable of moderate long-distance dispersal, but did not really address the issue of recruitment in this genus. The presence of flowers and seeds only illustrates the potential of seagrass species to reproduce by sexual means and is not indicative of the actual contribution but of the maximum potential contribution of sexual reproduction to population maintenance.

Flowering in *Posidonia coriacea* differs from that of *Heterozostera tasmanica*. Seagrasses from the genus *Posidonia* (Posidoniaceae) are monoecious with hermaphrodite flowers, containing both male and female organs, formed in a series of spikes on a long peduncle. Members of the genus *Heterozostera* (Zosteraceae) are also monoecious, however flowers are unisexual with male and female flowers occurring on different shoots and arranged alternately in two longitudinal rows on a flattened spike enveloped within a modified leaf sheath (Den Hartog, 1970; Kuo and McComb, 1989).

Spatial variability in densities of flowering shoots within a seagrass meadow may be indicative of environmental differences, shoot age (e.g. *T. testudinum*: Gallegos et al., 1992) or clonal (genetic) variation (Cook, 1983). For example, Inglis (2000b) analysed the spatial distribution flowers, seeds and seed banks in *Halodule uninervis* in intertidal sediments of North-east Queensland. He produced contour maps of flowers in a 1.75 m<sup>2</sup> grid of 0.25 m<sup>2</sup> cells, and seeds in a 4 m<sup>2</sup> grid and found flowering was very heterogeneous. Similarly, within the Posidoniaceae, small-scale patchiness of flowering shoots of *P. oceanica* also occurs sub-tidally within individual meadows in the Mediterranean (Buia and Mazzella, 1991) and

*P. australis* in eastern Australia (Inglis and Lincoln Smith, 1998). For the Zosteraceae, patchy distribution of flowering shoots within a meadow has been reported for two populations of *Z. capricorni* in eastern Australia (Conacher et al., 1994; Inglis and Lincoln Smith, 1998).

This paper describes the extent of sexual reproduction in *Posidonia coriacea* and *Heterozostera tasmanica* on Success Bank Western Australia, by determining the interannual and small-scale spatial variation in flower density and subsequent seed set over a 3-year period (1996–1998). The study specifically addresses four main research questions: (1) How much flowering is occurring in populations of *P. coriacea* and *H. tasmanica*? (2) What is the reproductive success, or how many flowers actually produce seeds? (3) Does the amount of reproduction and seed production vary among years? (4) Is sexual reproduction random or patchy in distribution within meadows of *P. coriacea* and *H. tasmanica*?

## 2. Materials and methods

### 2.1. Study location

This study was located within a mixed meadow of *Posidonia coriacea* and *Heterozostera tasmanica* on Success Bank, Western Australia (32°04'21.5" S, 115°42'43.5" E). The location was approximately 3 km from the coastline and had a constant depth of 6.5 m (tidal range = 0.25 m). Kendrick et al. (1999, 2000) have described the spatial distribution of *Posidonia coriacea*. Little has been published on *Heterozostera tasmanica* from this region and it has not been mapped because it has low leaf area indices and therefore is difficult to distinguish from bare sand (Kendrick et al., 2000). The variable vegetative morphology of *Posidonia coriacea* on Success Bank has been described by Campey et al. (2000).

### 2.2. Interannual variation in flowering frequency

Inflorescences (fertile shoots) of *Posidonia coriacea* and *Heterozostera tasmanica* were collected by divers on SCUBA from 1 m<sup>2</sup> quadrats sampled at 10 m intervals within a 100 m × 110 m grid over three flowering seasons (early summer—December 1996, 1997 and 1998). The perimeter was permanently marked at 10 m intervals with star pickets to enable the same grid to be sampled each year. Fruit development of *P. coriacea* and seed set in spathes of *Heterozostera tasmanica* were complete at the time of collection. Also, the percentage cover of vegetative shoots within each 1 m<sup>2</sup> quadrat was recorded. In the laboratory, the number of inflorescences per quadrat was determined for each species. To examine the extent of sexual reproduction in *P. coriacea* and *H. tasmanica* all fertile shoots within each quadrat were examined and the number of seeds, aborted seeds and spent unfertilised flowers were recorded. The total number of flowers was the sum of the three categories. The probability that a flower will set seed was calculated as a ratio of the seed set per inflorescence to the total number of flowers per inflorescence.

### 2.3. Spatial variation in flowering frequency

Geostatistics were used to analyse and model the spatial distribution of fertile shoots of *Posidonia coriacea* and *Heterozostera tasmanica* in 1 m<sup>2</sup> quadrats within the 100 m × 110 m

grid during 1996, 1997 and 1998. Comparisons among quadrats were made of estimates of density of fertile shoots separated by 10 m increments, in all directions on the grid, spaced up to 60 m apart (maximum lag distance; Rossi et al., 1992). Spatial pattern was evaluated using semivariance and block krigging. Semivariance is the variance between independent samples minus the covariance among samples separated by a distance  $h$ . Semivariograms were calculated using GEO-EAS version 1.2.1 software (Englund and Sparks, 1998). To obtain a reliable estimate of the variance at least 30 sample pairs should be taken at each of the distances for which a variance will be determined (Journal and Huijbregts, 1978). Linear or spherical models were fitted to the semivariograms to define the type of spatial structure and the range of spatial dependence. The spherical model had the following form:

$$\gamma(h) = C_0 + C \left[ \frac{3}{2} \cdot \frac{h}{a} - \frac{1}{2} \cdot \left( \frac{h}{a} \right)^3 \right]$$

where  $C_0$  = the localised discontinuity, or nugget variance,  $C$  = the sill—the localised discontinuity,  $h$  = lag distance and  $a$  = the range (Schotzko and O'Keefe, 1989). Spherical and linear models were fitted to semivariograms using the model of best fit and the non linear curve fitting program Mac Curve Fit (MCF 1.2.2; Raner, 1996).

Krigging was used to provide estimates of inflorescences per m<sup>2</sup> for unrecorded locations within the grid to enable the mapping of fertile shoot density within the area (Rossi et al., 1992). The models from the semivariograms were used together with the sampling data to calculate the optimum weights attributable to each sampling unit ( $w_1, \dots, w_n$ ), to estimate the inflorescence density ( $Z^*$ ) at an unsampled area (block-krigging):

$$Z^* = \sum_{i=1}^n w_i Z(x_i)$$

where  $n$  = number of samples,  $w_i$  = weight attributable to sample  $x_i$  calculated from semivariogram and where  $\sum_{i=1}^n w_i = 1$ , and  $Z(x_i)$  = inflorescence density at location  $x_i$ . Contour maps of fertile shoot density were then produced.

Spatial variation in density of inflorescences and seeds within 10 m × 10 m quadrats located 10, 20, 40 and 80 m apart was also examined in 1996. These larger 100 m<sup>2</sup> quadrats were used to determine if there was any significant difference in the number of fertile shoots in larger areas in comparison to the smaller 1 m<sup>2</sup> quadrats used above, at different distances from each other and at larger sampling units. Data was analysed using a one way ANOVA with distance as the fixed factor.

### 3. Results

#### 3.1. Interannual variation in flowering frequency

*Posidonia coriacea* flowered within the study location in 1996, 1997 and 1998 (Table 1). Similar total numbers of flowers (in 1.1 ha) were produced in 1996 ( $n = 7025$ ) and 1997

Table 1

Relative flowering frequency and seed set of *Posidonia coriacea* and *Heterozostera tasmanica* collected from a total of 110 quadrats of 1 m<sup>2</sup> within a 100 m × 110 m grid on Success Bank

	<i>Posidonia coriacea</i>			<i>Heterozostera tasmanica</i>		
	1996	1997	1998	1996	1997	1998
Seagrass cover (%)	30 (1.8)	35 (1.8)	33 (1.9)	22.0 (2.5)	23.2 (2.5)	19.5 (2.1)
Number of inflorescences per m <sup>2</sup>	3 (0.3)	3 (0.6)	1 (0.2)	0	4.6 (0.8)	0
Number of flowers per m <sup>2</sup>	63.8 (7.8)	70.1 (13.6)	18.1 (2.8)	0	67.1 (12.7)	0
Number of seeds per m <sup>2</sup>	12.9 (1.7)	14.6 (2.8)	4.1 (0.7)	0	59.9 (11.4)	0
Number of inflorescences sampled ( <i>n</i> )	346	363	134	0	502	0
Number of flowers per inflorescence	20.3 (0.4)	18.7 (0.5)	13.5 (0.5)	–	14.7 (0.4)	–
Number of seeds per inflorescence	4.1 (0.2)	4.5 (0.2)	3.4 (0.2)	–	13.1 (0.3)	–
Probability of a flower to set seed	0.20 (0.01)	0.22 (0.01)	0.24 (0.01)	–	0.89 (0.004)	–

Standard errors in parentheses.

(*n* = 7707), but flowering density decreased 4 fold in 1998 (*n* = 1809). A similar decrease was observed for mean numbers of inflorescences, flowers and seeds per m<sup>2</sup> (Table 1). The density of inflorescences was not closely related to seagrass cover, which remained constant throughout the study.

Approximately one-fifth of the flowers produced by *P. coriacea* in 1996, 1997 and 1998 set seed (Table 1). The reduced number of seeds set per inflorescence in 1998 was due to less flowers produced per inflorescence, and not to a reduction in the probability that a flower will set seed (Table 1). Probabilities of flowers setting seed increased by 0.04 (or 4%) between 1996 and 1998. Total seed production was also low relative to vegetative shoot recruitment in the study area of  $240 \pm 84 \text{ m}^{-2}$  per year (mean  $\pm$  S.E., *n* = 6).

In contrast to *Posidonia coriacea* which flowered every year, *Heterozostera tasmanica* only flowered in 1997 (Table 1). Small numbers of *H. tasmanica* flowers were observed in 1998, but these were not within the sampling area. The ratio of male to female flowers in 1997 was equal to one. The high number of seeds per inflorescence ( $13.1 \pm 0.33$ ) in comparison to flowers per inflorescence ( $14.7 \pm 0.4$ ) in 1997 indicated that there was a very high probability (89%) that *H. tasmanica* flowers would set seed (Table 1). Total seed production (Table 1) was also low relative to vegetative shoot recruitment in the study area of  $360 \pm 86 \text{ m}^{-2}$  per year (mean  $\pm$  S.E., *n* = 6).

### 3.2. Spatial variation in distribution of flowering frequency

Distribution of inflorescences of *Posidonia coriacea* within the grid differed over the 3 years sampled. In 1996, a spherical model provided the best fit to the semivariogram with a sill at approximately  $30 \pm 15 \text{ m}$ , indicating that inflorescence densities were spatially dependent and non-randomly distributed up to that sill from any point sampled (Table 2). The localized discontinuity (nugget variance) was high and accounted for about 68% of the

Table 2  
Summary of semivariogram models for *P. coriacea* and *H. tasmanica* inflorescences within the sampling grid on Success Bank for 3 years

Species	Year	Best fit model	r <sup>2</sup>	Y intercept or localized discontinuity	Slope	Range (m)
<i>Posidonia coriacea</i>	1996	Spherical	0.41	$C_0 = 0.52$ (0.20)	–	$a = 29.4$ (15.5)
	1997	Linear	0.24	$b = 1.00$ (0.03)	$a = 0.014$ (0.008)	Random
	1998	Linear	0.12	$b = 0.47$ (0.02)	$a = -0.006$ (0.006)	Random
<i>Heterozostera tasmanica</i>	1997	Spherical	0.86	$C_0 = 0.69$ (0.15)	–	$a = 29.4$ (15.5)

Standard errors in parentheses. These models are the best non-linear (spherical) and linear fits of semivariograms. The formula for the spherical model is given in Section 2.

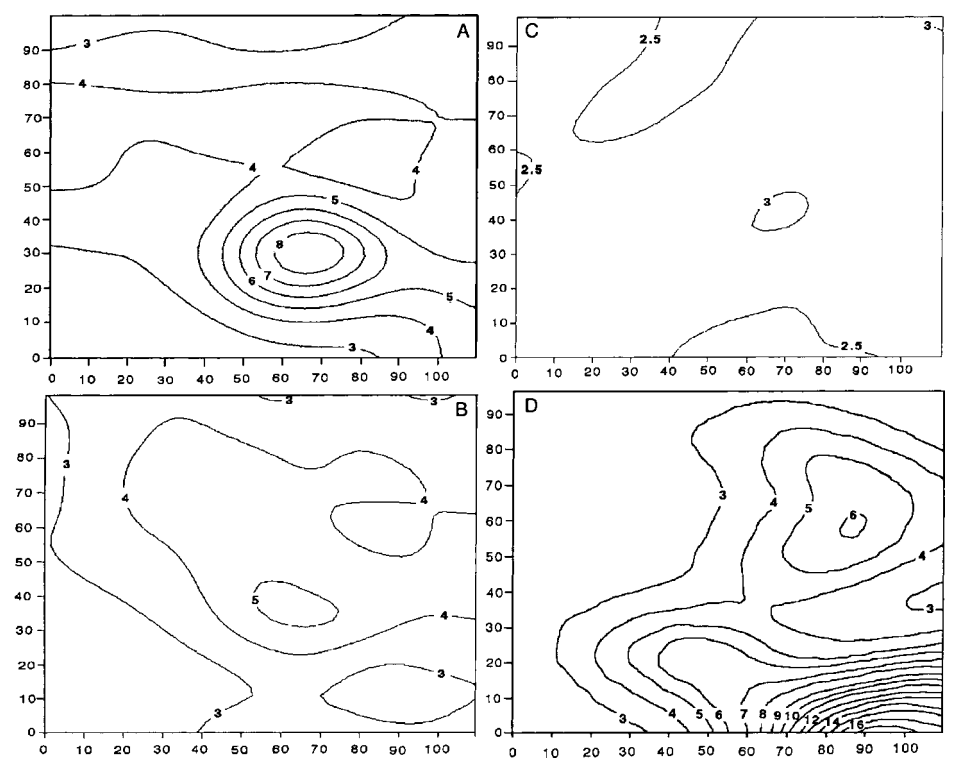


Fig. 1. Spatial distribution of *P. coriacea* inflorescences over the 1100 m<sup>2</sup> grid on Success Bank in (A) 1996, (B) 1997 and (C) 1998 and (D) of *H. tasmanica* fertile shoots in 1997 determined from block krigging. Density contour increments of one inflorescence per m<sup>2</sup>. X- and Y-axes are in meters distance east and north, respectively. The coastline of Western Australia is 2.5 km to the east of the grid.

semivariance at the sill, indicating that about 68% of the total variation was due to random or spatial variation less than the minimum distance between quadrats ( $<10$  m). A considerable amount of the variation was found between closely spaced points, indicating that at a scale 10 m or less, *Posidonia coriacea* inflorescences are patchily distributed.

No spatial dependence, or clustering of inflorescences, was found among inflorescence densities within the grid in 1997 or 1998. Inflorescences were randomly distributed, as indicated by the linear models and low slopes and low  $r^2$ -values fitted to both semivariograms (Table 2). The low slopes close to 0 suggest that samples close together were no more similar to each other than those further apart and hence spatially independent. There was more variance in inflorescence densities in 1997 than in 1998, when densities were greater, as indicated by a doubling of the localised discontinuity for 1997.

Density of inflorescences of *Posidonia coriacea* was low in all sampled years. Inflorescences were sparsely distributed over the entire  $100\text{ m} \times 110\text{ m}$  grid (1.1 ha). Krigged contour plots using the regression models (Table 2) showed that distribution of *P. coriacea* inflorescences varied both in space within a year and among the 3 years sampled (Fig. 1). The clustering of inflorescences observed within 30 m in 1996 (i.e. the sill; Table 2) represents the high inflorescence densities found in the south-east quadrant (over eight inflorescences per  $\text{m}^2$ ) for that year (Fig. 1A). In 1997, the distribution of inflorescences was more even, although the density was similar to 1996 (Fig. 1B). In 1998, inflorescence densities were much lower and inflorescences more evenly distributed across the grid (Fig. 1C).

In 1996, density of inflorescences in  $100\text{ m}^2$  samples located closer together are no more similar than those located further apart indicating that at this scale, no pattern is evident in the distribution of inflorescences at the study location. No significant differences in inflorescence densities were observed from  $100\text{ m}^2$  quadrats placed 10, 20, 40 and 80 m apart (Fig. 2, ANOVA:  $F = 0.889$ ,  $p = 0.476$ ,  $\text{df} = 3$ ). The mean inflorescence density was  $2.42 \pm 0.35\text{ m}^{-2}$  which is similar to  $3.0 \pm 0.3$  inflorescences per  $\text{m}^2$  recorded from the grid (Table 1).

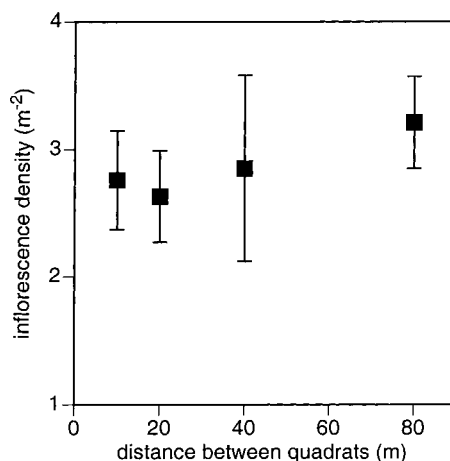


Fig. 2. Mean inflorescence density (inflorescences per  $\text{m}^2$ ) of *P. coriacea* in  $10\text{ m} \times 10\text{ m}$  quadrats separated by 10, 20, 40, and 80 m ( $\pm$ S.E.,  $n = 4$ ).



The distribution of fertile shoots of *Heterozostera tasmanica* in 1997 had significant spatial structure. A spherical model provided the best fit to the semivariogram, which attained the sill at  $27.9 \pm 3.6$  m, indicating that fertile shoots were spatially clustered within this bound (Table 2). The localised discontinuity was high at  $0.69 \pm 0.15$ , accounting for about 55% of the semivariance at the sill, indicating that about 55% of the total variation was due to random variation or unexplained processes acting at scales of less than 10 m (Table 2).

In contrast to the random distribution observed for inflorescences of *Posidonia coriacea* in 1997 (Fig. 1B), the distribution of fertile shoots of *H. tasmanica* was clumped within that year (Fig. 1D), similar to *P. coriacea* in 1996 (Fig. 1A). The highest densities of fertile shoots of *H. tasmanica* were observed in the south-east quadrant of the grid (17 inflorescences per  $\text{m}^2$ ), while most of the remaining areas of the grid had less than 3 inflorescences per  $\text{m}^2$ . No fertile shoots were observed within the grid in 1996 or 1998.

#### 4. Discussion

*Posidonia coriacea* and *Heterozostera tasmanica* differ greatly in flowering frequency, seed setting and seed density, suggesting that different reproductive strategies are utilised by each of the species. *P. coriacea* produced flowers each year, whereas in *H. tasmanica* flowering was more episodic and only occurred in one of the 3 years of this study (1997). Also the spatial distribution of fertile shoots varied across the 1.1 ha study area within a year and among years for both species. The probability of flowers to set seed varied significantly between *P. coriacea* (0.21) and *H. tasmanica* (0.90). Thus, although similar densities of flowers were observed for each species in 1997, the resultant seed density of *P. coriacea* was only 25% of that recorded for *H. tasmanica*. The percentage of *H. tasmanica* flowers setting seed was similar to that found in *Zostera capricorni* (90%) in offshore areas of eastern Australia (Conacher et al., 1994). *P. coriacea* (21%) had a lower percentage of flowers setting seed than *P. australis* (23–37%) located in more sheltered environments at nearby Penguin Island (Waycott et al., 1997).

Flowering densities of *Heterozostera tasmanica* and *Posidonia coriacea* were variable in space and time within the study area. A random model fitted the distribution of inflorescences of *P. coriacea* for 1997 and 1998 whereas a spatially patchy one did so for *P. coriacea* in 1996 and *H. tasmanica* in 1997. The causes of this spatial variation in flowering frequency are presently unknown but may be influenced by genetic variation (Cook, 1983), shoot age, distribution of active meristems for the production of shoots and inflorescences, or small-scale differences in the environment.

The high numbers of seeds produced by *Posidonia coriacea* in the 1.1 ha study area every year demonstrates its large annual reproductive effort. Each fruit is up to 2 cm long and 1 cm in diameter and the seed inside has substantial reserves for the first year of growth (Hocking et al., 1980) and is capable of settling rapidly (Orth, 1999) and recruiting (Kirkman, 1998). Although seeds of some species of the genus *Posidonia* rarely reach habitats suitable for recruitment (Larkum and West, 1982; Kirkman, 1985; Kirkman and Kuo, 1990; Kuo and Kirkman, 1996; Kirkman and Kirkman, 2000), we have observed new seedlings of *P. coriacea* each year on Success Bank. Vegetative growth alone cannot account for the increases in seagrass cover on Success Bank between 1972 and 1995 (Kendrick et al., 1999, 2000).



therefore recruitment from seedlings appears important for the persistence and expansion of *P. coriacea*.

*Heterozostera tasmanica*, although capable of high reproductive effort, differs from *Posidonia coriacea* as seedlings of *H. tasmanica* have not been observed on Success Bank. Kirkman and Kuo (1990) found high numbers of *H. tasmanica* seeds in the sediment, and fast colonisation by seedlings, at a site in Marmion, 34 km north of Success Bank. The absence of a seed bank of *H. tasmanica* on Success Bank implies that settlement of seeds is problematic. Success Bank is a high-energy environment, exposed to winter storms and ocean swell and the seeds may well be exported readily as bedload due to high bottom shear stress and sediment movement. It is also possible that the seeds are lost to predation (e.g. Fishman and Orth, 1996; Conacher et al., 1994).

In conclusion, *Posidonia coriacea* and *Heterozostera tasmanica* differed in their contribution of sexual reproduction to colonisation and establishment of seagrasses on Success Bank between 1996 and 1998. In *P. coriacea*, sexual reproduction can contribute to the maintenance of these populations, although interannual variation in flowering intensity suggests the relative contribution of sexual reproduction to meadow maintenance may vary considerably among years. Flowering in *H. tasmanica* contributes little to population maintenance. Although 1997 flower densities of *H. tasmanica* indicate there is potential for sexual reproduction to contribute to the meadow, the absence of flowers in 2 years of the study, the absence of a seed bank within the sediment and no observations of sexual recruits suggest that sexual reproduction contributes less to the maintenance of this population of *H. tasmanica*. The contribution of seedlings from sexual reproduction is small in comparison to annual shoot recruitment in existing patches and meadows of both species. Maximum seed production was <10% annual vegetative shoot production for *P. coriacea* and <20% for *H. tasmanica* between 1996 and 1998. Despite their low contribution relative to vegetative growth, seedlings are primarily important in the establishment of new patches and ultimately meadows.

## Acknowledgements

This study represents research towards a Ph.D. degree at the Botany Department, The University of Western Australia by M.L.C. It was funded by Cockburn Cement Pty. Ltd. and represents part of their environmental management program (EMP) for seagrasses. This research was also funded by an ARC Small Grant to GAK and DIW and a UWA Small Grant to DIW.

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