# A sediment bioturbator bottleneck to seedling recruitment for the seagrass *Posidonia australis*

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ABSTRACT: Bioturbating animals have the potential to influence the distribution and survival of seagrass seeds and seedlings within unvegetated substrates. Such disturbances could act as demographic bottlenecks, or restrictions, to seedling recruitment and impede population recovery in degraded systems. This study evaluated the influence of sediment bioturbators on seed settlement and seedling establishment for the seagrass *Posidonia australis* in temperate and subtropical areas of Western Australia (Cockburn Sound and Shark Bay). Initial benthic surveys recorded the density of sediment bioturbators as well as *P. australis* seeds and seedlings. The abundant bioturbators observed were the sand dollar *Peronella lesueuri* and the sea star *Archaster angulatus* in Cockburn Sound, and the heart urchin *Breynia desori* in Shark Bay. Surveys demonstrated an overlap in habitat use among bioturbators, seeds, and seedlings, and suggested potential negative seed–fauna interactions in areas where bioturbators were present and abundant. To test this relationship, field manipulative experiments measured the rate at which these bioturbators dislodged and moved both *P. australis* seeds (unburied and buried) and 1 yr old seedlings. Although all bioturbators dislodged and moved seeds on the sediment surface, only sand dollars and heart urchins dislodged and moved seeds (on average ~4 cm) buried within the sediment. Where high densities of bioturbators, such as sand dollars and heart urchins, exist, considerable impact on *P. australis* seeds would be expected. No animals dislodged 1 yr old seedlings. Sediment bioturbators act as an important, but often overlooked, bottleneck to seedling recruitment and recovery of degraded seagrass communities.

KEY WORDS: Bioturbators · Seeds · Seedling recruitment · Restoration · Seagrass · *Posidonia australis*

## INTRODUCTION

Seeds and seedlings are critical stages in the life history of seagrasses, particularly when the stability, persistence, and recovery of populations are dependent on seedling recruitment (Kendrick et al. 2017). Because early demographic stages are associated with high mortality rates, they may be considered demographic 'bottlenecks' which can limit recruitment within populations (Bond 2008, James et al. 2011, Statton et al. 2017). Seedling recruitment may be particularly rare in degraded systems even after the conditions prompting the degradation have been remedied (Suding et al. 2004). Once vegetation has been lost, changes in micro-climate, nutrient availability, hydrology, hydrodynamics, and predator–prey and/or plant–herbivore interactions can limit seed or seedling survival (Janzen 1971, Harper 1977, Eriksson & Ehrlen 1992, Fishman & Orth 1996, Holbrook et al. 2000, Wenny 2000, Orth et al. 2002, 2006b, 2007, Alagna et al. 2013, Darnell & Dunton 2015, Manley et al. 2015). In the marine environment,

benthic detritivores and scavengers that are obligate bioturbators of bare substrate are an additional threat to newly settled seagrass seeds and seedlings (Dumbauld & Wyllie-Echeverria 2003, Valdemarsen et al. 2011, Statton et al. 2012). Seagrass meadows have become increasingly degraded from human disturbances (Orth et al. 2006c, Waycott et al. 2009), resulting in unvegetated substrates where bioturbating fauna can potentially play a major role in influencing seed settlement and seedling recruitment as environmental conditions improve. Therefore, a clear understanding of how these seed– and seedling–fauna interactions influence early recruitment success is a critical step in providing appropriate management approaches to improve recovery and regeneration of lost seagrass habitat.

Bioturbation, the biological reworking of sediments, can pose a significant constraint on seedling recruitment, and thus on the natural regeneration or restoration of seagrass communities (Suchanek 1983, Philippart 1994, Meysman et al. 2006, Statton et al. 2012). Although bioturbators may not directly consume seeds or seedlings, disturbance of the sediment may uproot, bury, or damage them. Such disturbances, however, may not always be harmful or could result in differing outcomes depending on the seagrass life-stage. For instance, polychaete and crustacean deposit feeders have been shown to positively influence seedling recruitment through shallow burial of seeds (Luckenbach & Orth 1999, Blackburn & Orth 2013) but negatively influence seedling establishment through deep burial or light limitation (Dumbauld & Wyllie-Echeverria 2003, Valdemarsen et al. 2011). Several studies have suggested that polychaete bioturbators may have a profound impact on seagrass meadow distribution and health for *Zostera* spp. (Davis & Short 1997, Hughes et al. 2000, Delefosse & Kristensen 2012), but relatively few studies have explored the impact of other bioturbator assemblages (for example crustaceans, Molenaar & Meinesz 1995, Dumbauld & Wyllie-Echeverria 2003) on key demographic shifts of other seagrass species with different growth habits than *Zostera* spp.

Bioturbators are a diverse and active group of organisms with an equally diverse range of behaviors that disturb the sediment. Estimates of bioturbation on a global scale suggest that bioturbating fauna may rework enough sediment in a year to bury metropolitan London in 13 km of sediment (Teal et al. 2008). Different species will, however, rework or scour sediment differently in search of food, or burrow into the sediment for refuge (Kristensen et al. 2012). Polychaetes in coastal marine environments irrigate or

consume sediments and have been reported to rework 91–114 $cm^3$ $m^{-2}$ $d^{-1}$ $ind.^{-1}$ (Valdemarsen et al. 2010). Spatangoida urchins push themselves through the upper 5 cm of the sediment as they feed and have been reported to rework up to 500 $cm^3$ $m^{-2}$ $d^{-1}$ $ind.^{-1}$ (Lohrer et al. 2005). A diverse global bioturbator community could thus have a substantial, but variable, impact on aquatic vegetation communities also inhabiting sediments.

For the seagrass *Posidonia australis*, a dominant seagrass species found in the temperate coastal waters of southern Australia, seeds are important for the dispersal of seedlings to remote and/or uncolonized habitat, but are also integral to the population dynamics and genetic composition of existing populations (Kendrick et al. 2012, 2017, Sinclair et al. 2014). *P. australis* is a slow-growing and long-lived, 'persistent,' foundation habitat species that flowers annually to produce positively buoyant fruit capable of dispersing large distances before releasing a large (1.5–2.0 cm) and directly developing seed (Ruiz-Montoya et al. 2012, Kilminster et al. 2015, Statton et al. 2017). For the purposes of this paper, the term 'seed' will refer to this recently released propagule without a root-rhizome network anchoring it into the sediment. A 'seedling' will refer to a propagule with a root-rhizome network within the sediment. 'Seedling establishment' will refer to the process by which a seed transitions into a seedling, and 'seedling recruitment' will describe the entire process by which a seed ultimately enters the adult, reproductive population.

Because *P. australis* seeds grow from the moment of release, they have a narrow window of time to grow root anchors. Statton et al. (2017) suggested the majority of seed mortality in sheltered and moderately exposed locations occurs in <1 mo, and hypothesized that this mortality resulted from abundant echinoderm populations at these locations. Based on the shallow tracks and pits which Statton et al. (2017) observed echinoderm bioturbators to generate in the sediment at depths suitable for seed settlement, they suggested that these animals dragged or pushed seeds out of the sediment and away from restoration plots. Unlike previously studied bioturbator species that compromised seed and seedling survival through burial below a previously determined critical sediment depth, these bioturbators could potentially pull seeds and seedlings out of the sediment. For *P. australis*, uprooting seeds has profound implications on seed survival, as shoot development can make a seed positively buoyant in as little as 2 wk (A. J. Johnson pers. obs., and see Fig. S1 in the Sup-

plement at www.int-res.com/articles/suppl/m595p089_supp.pdf). Bioturbator foraging which pushes seeds out of the sediment during critical early life stages could thus have a strong effect on *P. australis* seed survival, as seeds pushed out from the sediment or prevented from anchoring themselves to the sediment with roots will float away from suitable habitat. In addition, because *P. australis* exhibits a 'phalanx' growth style of densely packed shoots (Lovett-Doust 1981), seedling recruitment is assumed most likely to occur in unvegetated areas between or away from adults that potentially compete with seeds for limiting resources. Similarly, the short-term survival of *P. australis* seeds in bare sand was 3–5-fold higher than within *P. australis* meadows abundant with seed predators (Orth et al. 2002, 2006d, 2007). Thus, seed settlement and seedling recruitment may be limited in space and time to bare areas that are also suitable habitat for sediment bioturbators in search of food or refuge.

In this study we evaluated the interaction between sediment bioturbators, recently settled seeds, and 1 yr old seedlings of the seagrass *P. australis* using both laboratory and field experiments. The objectives were to (1) survey the bioturbator species present in both natural and restoration settings, their densities, and their spatial overlap with *P. australis* seeds and seedlings in temperate western Australia; (2) quantify the rate and categorize the type of movement for each sediment bioturbator; (3) determine if bioturbators are capable of dislodging and moving seeds that are settled on the surface or pushing seeds buried in the sediment out of the sediment; and (4) determine if bioturbators are capable of dislodging 1 yr old seedlings. By evaluating the interaction between bioturbators and recently settled seeds and 1 yr old seedlings in this way, we expected to find a suite of bioturbators that cause a significant bottleneck to seedling recruitment and thus also to the recovery of degraded *P. australis* communities.

## MATERIALS AND METHODS

### Study sites

Our research was conducted within 2 embayments (Fig. 1) with several sites in each: Cockburn Sound (Cockburn Sound East, Owen Anchorage North, Owen Anchorage Central, Owen Anchorage South, and Carnac Island) and Shark Bay (Useless Loop and Guichenault Point), Western Australia. Cockburn Sound (32° 8′ 7.28″ S, 115° 43′ 53.93″ E) and the

surrounding area is a temperate semi-enclosed embayment near Perth and mid-range in the distribution of *Posidonia australis* along the coast of Western Australia. Shark Bay (26° 6′ 48.95″ S, 113° 24′ 42.05″ E) is a shallow, subtropical embayment, and represents a population of *P. australis* near its northernmost limit on the west coast of Australia. Survey sites and experimental trials focused on bare sandy areas adjacent to existing meadows of *P. australis* and at 2–4 m depth. These sites are part of ongoing seagrass recovery and restoration programs.

### Study design

To achieve the objectives outlined above, 4 separate but linked investigations were implemented as follows. (1) Surveys were conducted to establish the relative abundance of bioturbators and their overlap in distribution with seeds and seedlings of *P. australis*. (2) Observations of the movement of the 3 most abundant bioturbators (Fig. 2), i.e. the sand dollar *Peronella lesueuri* (Agassiz 1841) and sea star *Archaster angulatus* (Müller & Troschel 1840) in Cockburn Sound, and the heart urchin *Breynia desori* (Gray 1851) in Shark Bay, were measured in laboratory and field environments. (3) *In situ* experiments were then conducted to estimate the disturbance and disruption of bioturbator movement on seeds of *P. australis*. (4) *In situ* experiments were conducted to determine if 1 yr old seedlings with more developed root structures were disturbed by the movement of sand dollars and sea stars.

### Survey of fauna and recently settled seedlings

To measure the overlap and abundance of sediment bioturbators and *P. australis* seeds and seedlings, we surveyed 5 bare sandy areas representing areas of potential seedling recruitment at 2 locations, Cockburn Sound and Shark Bay, for suspected bioturbators and *P. australis* seeds and seedlings in autumn 2016. Suspected bioturbators were animals impacting the upper 2 cm of sediment through their movement. Recently settled *P. australis* seeds are ~2 cm long and may already maintain a ~1 cm tall shoot, making them easily identifiable on the sediment surface or shallowly buried (Statton et al. 2017). Individual plants with 1 or 2 shoots were identified as 1 yr old seedlings. Four sites in Cockburn Sound previously identified in a large-scale restoration program were surveyed: Owen Anchorage North, Central,
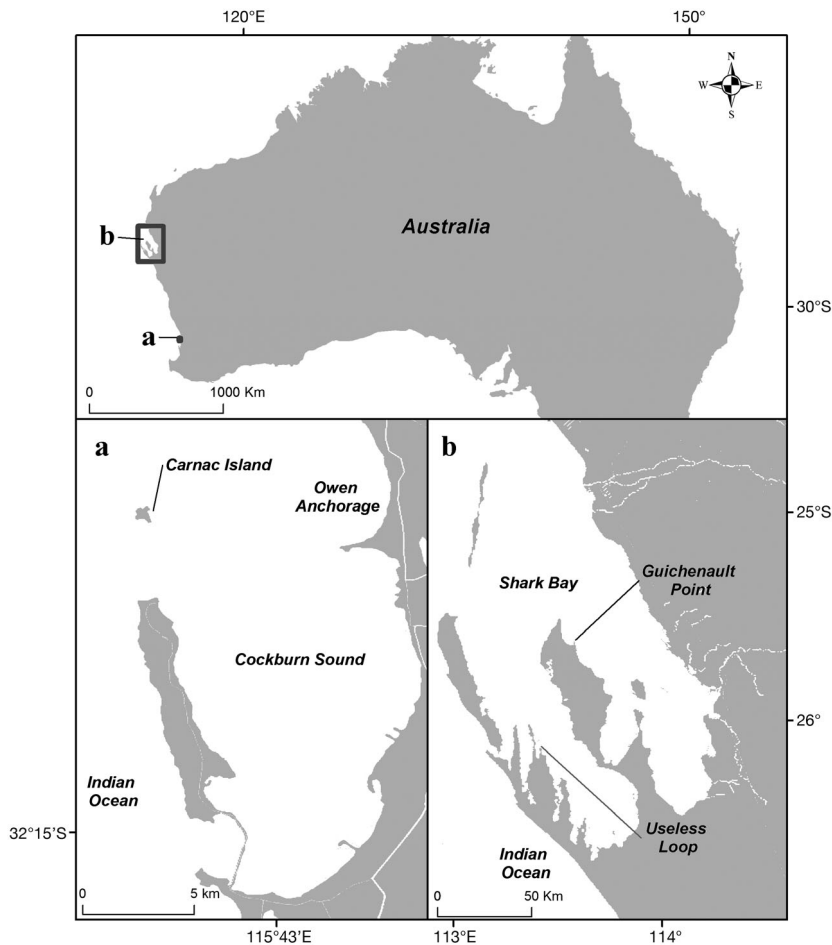
Fig. 1. Survey and experimental locations along the west coast of Australia, in (a) Cockburn Sound and (b) Shark Bay

and South, and Cockburn Sound east, and 1 unvegetated reference site on the shoreward, eastern side of Carnac Island. In Shark Bay, 3 sites were selected within Useless Loop, which were also part of ongoing restoration trials, and 2 bare sandy reference sites at Guichenault Point. Reference sites at both locations were adjacent to flowering *P. australis* meadows, and were included in the survey because each site potentially experiences less benthic bioturbating fauna than the restoration sites. At each site, 10 × 1 m transects (n = 5) were randomly assigned within bare sediments adjacent to *P. australis* meadows. Divers swam along these transects with a 1 m bar and recorded all animals on the surface and just below the sediment surface by sight and gently patting the sediment surface within 1 m of the transect. For seed and seedling counts, we conducted the survey in December after *P. australis* seed release to record the number of recently settled seeds and ~1 yr old seedlings (Statton et al. 2013).

## Animal movement

### Laboratory experiments

To estimate the relative intensity with which the most disruptive, mobile, and abundant sediment bioturbators disturb the sediment surface, we conducted movement experiments within controlled laboratory conditions which allow the collection of more detailed information on bioturbator movement through time than would be feasible over the duration of *in situ* experiments on SCUBA. Sand dollars were selected for these detailed measurements of movement, as they are known to move while partially buried within the upper ~1 cm of the sediment, and have been recorded at densities as high as 6 ind. m$^{-2}$ in Cockburn Sound (Forehead & Thompson 2010). Seven sand dollars were collected and placed within 2 recirculating 1800 l aquaculture tanks containing 2 tubs (0.5 m$^2$) filled with sediment to 20 cm below the water line. After sand dollars were acclimated to tank conditions for 24 h, the sand dollars were positioned at the end of each tub and small plastic position markers were placed behind the sand dollars every 2 h for 6 h and again the following morning. The linear distance (cm) between position markers was then measured. The sand dollars were tracked over 3 d, and position markers were repositioned each day.

Because measuring the linear distance between plastic position markers placed behind sand dollars at regular intervals did not account for their nonlinear movements, 3 additional sand dollars were collected from Cockburn Sound and placed within 1 of 3 tubs (as described above) and acclimated for 24 h before estimating their nonlinear movement through time. After acclimating, each sand dollar was moved into an identical tub in which the sediment was covered with an additional 1 cm of fine white silica sediment. The underlying sediment was red-orange in color for maximum contrast when bioturbation was observed. Each tub was divided in half (2 × 0.25 m$^2$ areas), and 1 sand dollar was placed into 1 half of each tub while the adjacent half received no sand dollar and served as a control (i.e. no sediment disturbance from sand dollars). A position marker was placed behind the sand dollar as it was introduced into the tank. Every 6 h, a photo of all 3 tubs was taken, and the percent of disturbed fine sediment in each tub over which the
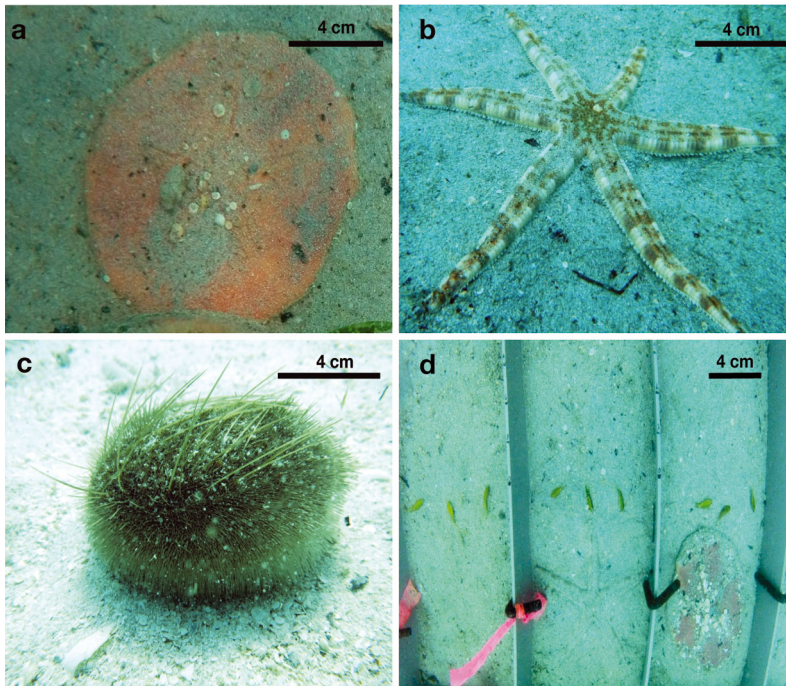
Fig. 2. Sediment bioturbators common in surveys in Cockburn Sound and Shark Bay as well as the experimental lanes used to guide each of these animals toward *Posidonia australis* seeds: (a) sand dollar *Peronella lesueuri*, (b) sea star *Archaster angulatus*, (c) heart urchin *Breynia desori*, and (d) the experimental design placing a sand dollar (far right lane), and a sea star (center lane) in front of 3 green *P. australis* seeds placed on the sediment surface in their path and a control lane with 3 seeds but without a sediment bioturbator (far left lane)

sand dollars had moved, as well as the linear distance the sand dollars had traveled, was recorded for 24 h.

## Field experiments

The most abundant bioturbators recorded in the transect surveys, sand dollars *P. lesueuri* and sea stars *A. angulatus* in Cockburn Sound, and heart urchins *B. desori* in Shark Bay, were selected for detailed estimates of their movement rates. *In situ* estimates of the rate at which sand dollars, sea stars, and heart urchins move were recorded during bioturbator experiments on SCUBA (see below). These experiments used plastic dividers (7.5 cm height, 50 cm length) inserted into the sediment to guide individuals of each bioturbator species from a fixed point, one end of the plastic dividers, toward 3 seeds placed across each lane 20 cm in front of this point and within the path generated by the dividers for each bioturbator (Fig. 3). An experiment was concluded when an animal had either moved beyond all of the seeds in its path or moved 50 cm and thus beyond the plastic dividers guiding its movement. The rate at which a given ani-

mal moved during the experiment was calculated by measuring the duration over which each experiment occurred and the total distance each animal moved during the experiment, from initial placement in the experiment at a fixed location to the animal's position at the end of the experiment. Because heart urchins move beneath the surface and more slowly than sand dollars and sea stars, *in situ* observations of heart urchin movement within a day were not feasible. As a result, heart urchins were left for 24 h, and the distance the animals moved over this time period was recorded.

To estimate how frequently sand dollar and sea star populations may disturb *P. australis* seeds, the density, size, and movement of each bioturbator species was multiplied by the mean density of seeds at a survey location with high abundances of both species, namely Owen Anchorage Central (OAC). The mean rate at which individuals moved in experiments was scaled to a daily rate and multiplied by the mean width for each species to calculate a mean area that individuals of each species would disturb in a day. This calculated disturbance rate was then multiplied by the density of each species at OAC to calculate the area the sand dollar or sea star population at OAC would disturb in a given day. This disturbed area was then multiplied by the mean number of *P. australis* seeds m$^{-2}$ counted at OAC to estimate how many natural seeds each species would disturb at this location in a given day. In order to estimate how many seeds these animal populations would disturb daily in theoretical 50 m$^2$ restoration plots at OAC in Cockburn Sound or at Useless Loop (UL1) in Shark Bay, the area each population of bioturbator would disturb daily was multiplied by 100 seeds m$^{-2}$, the seeding density used by Statton et al. (2017) as a proposed seeding density.

## Field bioturbator experiments

### Recently settled seeds

To evaluate the impact of sediment bioturbator movement on *P. australis* seeds recently settled on the sediment surface and also buried within the
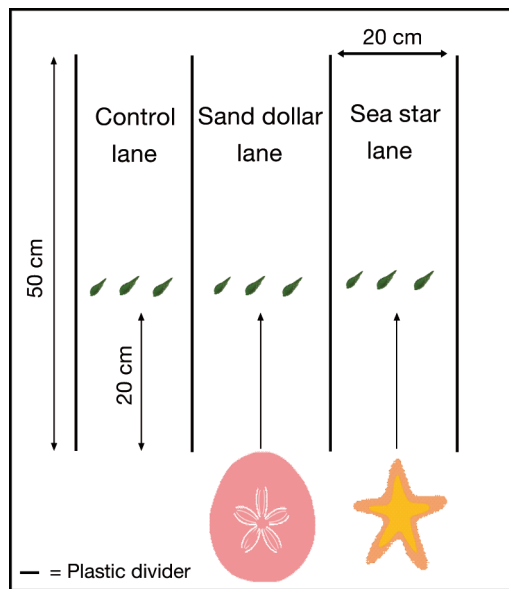
Fig. 3. Schematic of the *in situ* experiments guiding bioturbators suspected of impacting seed settlement and seedling recruitment. Plastic dividers (7.5 cm height × 50 cm length) were inserted into the sediment 20 cm apart to generate 3 'lanes.' Three *Posidonia australis* seeds were then placed 20 cm down the length of each lane on the sediment surface (green teardrop shapes). A sediment bioturbator (sea star or sand dollar) was introduced at the base of each lane, 20 cm from the seeds, and guided toward the seeds placed in their path. If the animals impacted any seed as they moved, the interaction was categorized as 'disturbed.' If no seeds moved over the course of the interaction, the interaction was categorized as 'undisturbed.' This experiment was repeated with 3 seeds buried 1 cm into the sediment and later with a single 1 yr old seedling placed 20 cm down the length of each lane. Cartoons were sourced from the Integration and Application Network (Kleine 2010) and www.clker.com

sediment, *in situ* field experiments were conducted at both Cockburn Sound and Shark Bay. We tested the influence of the sand dollar *P. lesueuri* and the sea star *A. angulatus* in Cockburn Sound, and the heart urchin *B. desori* in Shark Bay. Raceways or lanes were constructed in bare sand using 2 plastic dividers (7.5 cm height, 50 cm length) inserted into the sediment 20 cm apart. Individual bioturbators were placed at the start of a raceway and 3 recently settled seeds were placed across each row 20 cm from the base of the lane (Figs. 2d & 3). As each animal moved along the lane, the impact of the animal's movement on the seeds' state was categorized as either disturbed (uprooted or buried as a consequence of the bioturbator's movement) or undisturbed (unaffected or unimpacted by the bioturbator's movement). Control lanes were also established alongside lanes with bioturbators to evaluate if currents or

alternative processes may also have moved seeds. If after 3 min a sand dollar or sea star had not moved from the start of the lane, the animal was deemed unresponsive and replaced with an individual of the same species that was mobile. An experiment was concluded when an animal had either moved beyond all of the seeds or moved >50 cm and thus beyond the plastic dividers guiding its movement. Because heart urchins move beneath the sediment surface and more slowly than sand dollars and sea stars, heart urchins were left within the experimental lane for 24 h before evaluation. The distance a seed was moved, either by animal or other processes, was measured in 3 cm increments up to 15 cm from the seeds' starting position. Seven sea stars, 8 sand dollars, and 9 heart urchins were guided toward seeds placed on the sediment surface. Nine animals of each species were guided toward seeds buried 1 cm into the sediment. After all animals had finished interacting with the seeds, the length, width, and height of each animal was recorded. Additionally, to determine if animals interacted with seeds when the former were not handled or guided into seeds by lanes, we placed seeds 5 cm in front of unhandled and moving sand dollars and sea stars and then recorded the seed state after the interaction.

### One year old seedlings

To test if bioturbators were able to disturb 1 yr old seedlings, plastic divider raceways (as described above) were also constructed around 1 yr old seedlings in Owen Anchorage. Nine sand dollars and 9 sea stars were introduced at the base of each lane and guided toward a single 1 yr old seedling centered 20 cm from the start of each lane. Whether the seedling was disturbed or undisturbed was then recorded, and, if disturbed, the distance that the animal moved the seedling was measured. This experiment was not conducted with heart urchins in Shark Bay, as 1 yr old seedlings were not present within the experimental area.

### Statistical analysis

Analysis of variance (ANOVA) was used to determine if significant differences in the densities of sand dollars, sea stars, and *P. australis* seeds and seedlings occurred between surveyed locations in Cockburn Sound. Spearman's rank correlation coefficients were then used to test if any statistically significant rela-

tionships existed between the mean number of bioturbators and either the mean number of *P. australis* seeds or seedlings observed at survey locations in Cockburn Sound. Separate correlations tested if the mean number of seeds counted at a location was related to the mean number of sand dollars or sea stars also observed at that location. Additional correlations tested whether the mean number of 1 yr old seedlings counted at a location was related to the mean number of sand dollars or sea stars at that location. These correlations were not intended to determine causality between animal densities and seed or seedling densities, but rather to determine if any statistically significant relationship exists between *in situ* sediment bioturbator populations and the presence of early seagrass life stages. Spearman's rank correlation was used as a non-parametric, rank-based alternative to Pearson's product moment correlation, as the surveyed animal and plant densities were not normally distributed. Correlation analysis was not conducted with heart urchins in Shark Bay, as heart urchins were not recorded in the vicinity of *P. australis* seeds outside restoration areas.

To determine if sand dollars scouring the fine sediment in experimental tubs disturbed more of the upper 1 cm of the sediment than in control areas, differences in the percentage of sand disturbed between sand dollar and control areas were analyzed with a repeated measures ANOVA.

Because seeds or seedlings placed in experimental lanes were categorized as disturbed (uprooted or buried) or undisturbed (left in state), odds ratios were used to compare the likelihood of a seed or seedling being disturbed in lanes with bioturbators relative to the likelihood of disturbance in lanes without bioturbators for each species of bioturbator evaluated. An odds ratio of 1 would indicate seeds or seedlings were as likely to be categorized as disturbed in lanes with bioturbators as in lanes without bioturbators. Fisher's exact tests were then used to estimate if observed disturbance was significantly different than expected (i.e. the disturbance would be the same) in animal and control lanes. To test if seeds or seedlings in experimental lanes with animals moved more than seeds or seedlings within control lanes, Welch's *t*-tests were used to determine if significant differences in the mean distance seeds or seedlings moved existed between lanes with or without animals. Welch's test was used, as the variance between animal and control treatments was uneven.

A type I error rate of 0.05 was established for all statistical tests. Spearman's rank correlation coefficients were conducted using the cor.test function from the 'stats' R core package (R Development Core Team 2015). Odds ratios and Fisher's exact tests were calculated with the oddsratio.wald function within the 'epitools' package (Aragon 2012). All statistics were performed in R statistical analysis software (R Development Core Team 2015).

## RESULTS

### Survey of fauna and recently settled seedlings

Surveys of bioturbating animals recorded the highest densities of the sea star *Archaster angulatus* and the sand dollar *Peronella lesueuri* in Cockburn Sound East and the lowest densities at Carnac Island. Blue swimmer crabs *Portunus armatus* were also observed at Owen Anchorage South but were not abundant (n = 3) or observed at other locations. At Useless Loop in Shark Bay, the heart urchin *Breynia desori* occurred at the highest densities. Hermit crabs (*Pagurus* spp.), decorator urchins *Tripneustes gratilla*, and blue swimmer crabs were also recorded at Useless Loop. Only 1 hermit crab (*Pagurus* sp.) and several molts of blue swimmer crabs were observed at Guichenault Point.

In Cockburn Sound, the most abundant bioturbating species disturbing the upper centimeters of sediment were *P. lesueuri* and *A. angulatus.* Their densities varied significantly, however, between sites (Fig. 4a; $F_{4,20} = 32.9$, p < 0.001; $F_{4,20} = 14.5$, p < 0.001; Tables S1 & S2 in the Supplement). Sand dollars were present in Cockburn Sound East (8.6 ± 1.6 [SE] ind. transect$^{-1}$), OAC (7.8 ± 1.3 ind. transect$^{-1}$), and Owen Anchorage North (1.6 ± 0.6 ind. transect$^{-1}$). Sea stars were also present with sand dollars at OAC (11 ± 1.3 ind. transect$^{-1}$) and Cockburn Sound East (2.0 ± 1.6 ind. transect$^{-1}$), but were the dominant bioturbator present at Owen Anchorage South (8.6 ± 0.2 ind. transect$^{-1}$).

Recently settled *Posidonia australis* seeds were found at significantly different densities (Fig. 4b; $F_{4,20} = 94.9$, p < 0.001; Table S3) at sites surveyed around Cockburn Sound. Carnac Island and Owen Anchorage South recorded the highest densities of seeds transect$^{-1}$ (94 ± 17 and 71 ± 8.4, respectively); while Owen Anchorage North (11 ± 2.6) and OAC (4.6 ± 1.8) and Cockburn Sound East (0) recorded far lower densities. One year old seedlings also varied significantly in density across sites ($F_{4,18} = 8.73$, p < 0.001; Table S4). OAC had the highest number of seedlings transect$^{-1}$ (9.4 ± 2.0), while Cockburn Sound East (1), Owen Anchorage South (3.0 ± 0.95),
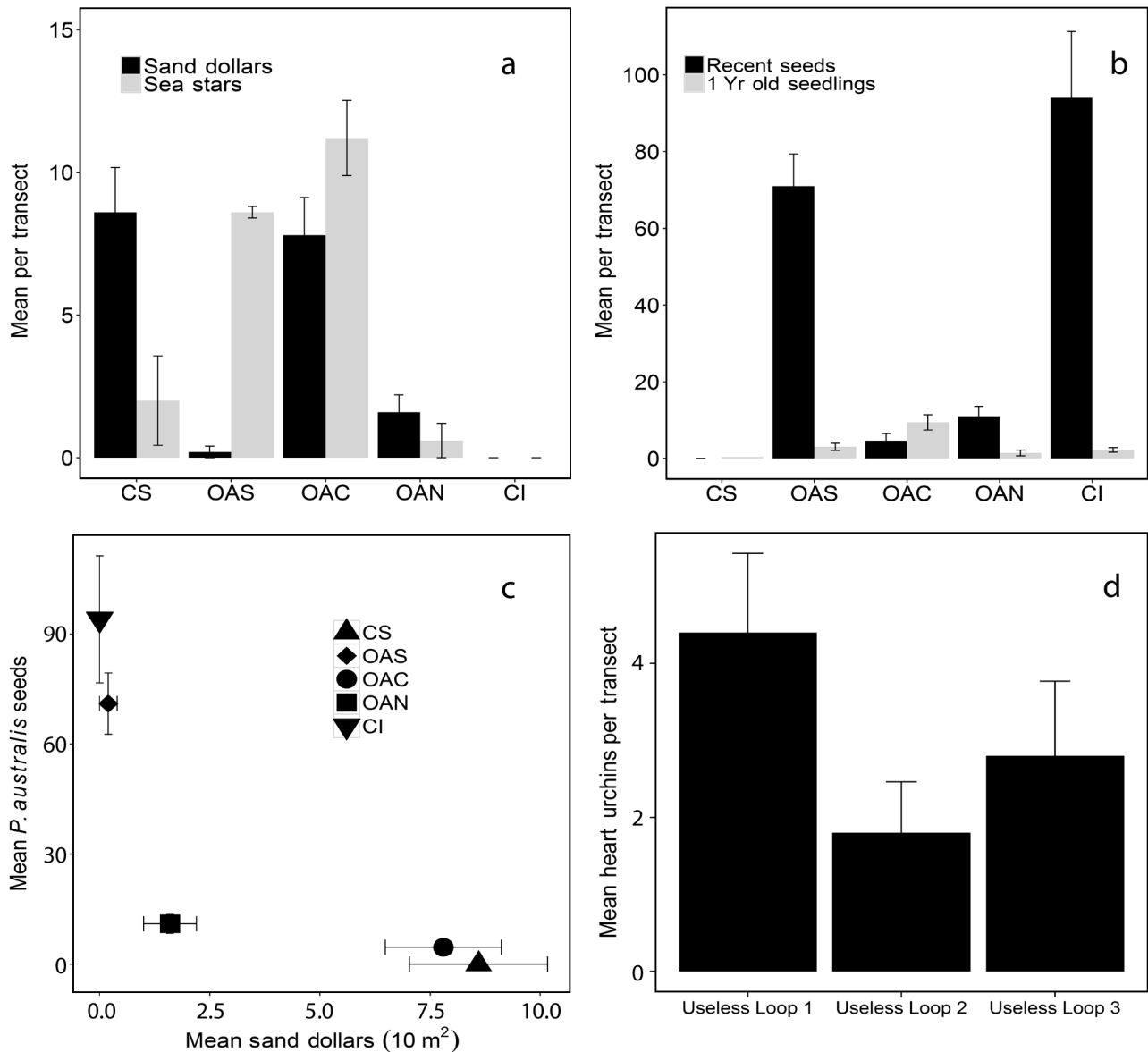
Fig. 4. Mean ± SE number of (a) sand dollars and sea stars and (b) *Posidonia australis* seeds and seedlings per transect (10 m², n = 5) at survey sites around Cockburn Sound. (c) Relationship between the mean density of sand dollars and seeds at the surveyed sites. (d) Mean ± SE number of heart urchins present at Useless Loop in Shark Bay. Heart urchins were absent from Guichenault Point. CS: Cockburn Sound, OAS: Owen Anchorage South, OAC: Owen Anchorage Central, OAN: Owen Anchorage North, CI: Carnac Island

Carnac Island (2.2 ± 0.58), and Owen Anchorage North (1.4 ± 0.75) exhibited lower densities.

*P. australis* seeds and seedlings were found together with bioturbating fauna within Cockburn Sound and Owen Anchorage, but not at Carnac Island (Fig. 4b). A significant negative correlation was detected between the density of sand dollars at a survey site and the density of seeds at that site (rho = −1, S = 40, p = 0.02, Fig. 4c, Table 1). This correlation suggests the potential for a negative relationship between sand dollar density and seed settlement at

the surveyed locations. The abundance of recently settled seeds was lowest at sites with high sand dollar densities in Cockburn Sound east and OAC, whereas the highest abundance of recently settled seeds occurred at sites with low densities of sand dollars (Carnac Island and Owen Anchorage South). No significant correlation, however, was detected between the density of sand dollars and the number of 1 yr old seedlings at a surveyed location or between the density of sea stars and either the number of seeds or seedlings at a surveyed location (Table 1).

Table 1. Spearman's rank correlation coefficients between the mean number of sand dollars or sea stars at a surveyed location and the mean number of *Posidonia australis* seeds and seedlings observed at that location. *Significant at p < 0.05

| Bioturbator | Variable | S | rho | df | p |
|---|---|---|---|---|---|
| Sand dollars | Seeds | 40 | −1 | 3 | 0.02* |
| | Seedlings | 26 | −0.3 | 3 | 0.7 |
| Sea stars | Seeds | 30 | −0.5 | 3 | 0.4 |
| | Seedlings | 8 | 0.6 | 3 | 0.6 |

At Useless Loop, in Shark Bay, the most abundant bioturbator was the heart urchin *B. desori,* reworking the upper 2–4 cm of sediment. During surveys, heart urchins were found at low densities (2 ± 0.4 ind. transect$^{-1}$ or 0.18 ind. m$^{-2}$; Fig. 4d) at all sites in Useless Loop, but have been found at much higher densities (2–3 m$^{-2}$, J. Statton pers. obs.). Heart urchins were absent from Guichenault Point. Only 2 recently settled *P. australis* seeds were observed at Guichenault Point. No *P. australis* seeds or seedlings were found at Useless Loop.

## Animal movement

### Laboratory experiments

The 7 sand dollars removed from Cockburn Sound and tracked within tanks moved 2.4 ± 4.2 cm h$^{-1}$ (range: 0–26 cm h$^{-1}$). These sand dollars in tanks moved substantially less than sand dollars in the field (~13 ± 4.8 cm h$^{-1}$, n = 9).

Over 24 h, the 3 sand dollars placed in tanks with fine sediment covering the surface disturbed ~0.15 m$^2$ (55 ± 10%, n = 3, Fig. 5) of the sediment surface, and disturbed significantly more of the upper 1 cm of fine sediment relative to control tanks without sand dollars ($F_{1,27}$ = 16.6, p < 0.001).

### Field experiments

Rates of animal movement and dimensions of animals calculated from field experiments indicate that all 3 species interacted with the upper 1–4 cm of sediment over the course of the experiment. Sand dollars partially buried themselves within the sediment (~1 cm) and were 2.2 ± 0.2 cm tall, 13 ± 0.3 cm wide, and 15 ± 0.2 cm long and moved on average 13 ± 4.8 cm h$^{-1}$ with a maximum recorded rate of



Fig. 5. Sand dollars placed in tanks covered in ~1–2 cm of fine sediment. The area over which sand dollars disturbed was monitored every 6 h over 24 h

82 cm h$^{-1}$. Sea stars moved primarily over the surface of the sediment and were 1.1 ± 0.02 cm tall, 17 ± 0.2 cm wide, and 18 ± 0.3 cm long and moved approximately 33 ± 8 cm h$^{-1}$ with a maximum recorded rate of 90 cm h$^{-1}$. Heart urchins were 3.7 ± 0.8 cm tall, 6.4 ± 0.1 cm wide, and 8.6 ± 0.1 cm long. After handling the urchins to introduce them at the base of a lane, all urchins immediately buried themselves ~4 cm within the sediment. Urchins then moved within the sediment for an average distance of 29.3 ± 0.3 cm (range: 23–35 cm d$^{-1}$, ~1.2 cm h$^{-1}$) within a day.

Measurements of sand dollar movement in laboratory conditions and *in situ* suggest that individual sand dollars could disturb ~0.15 and 0.4 m$^2$ d$^{-1}$, respectively, and their populations could disturb 6–16 m$^2$ of the survey area and 3–8 seeds, or 13–35% of all recorded seeds, daily at the densities recorded at OAC. Individual sea stars moving across the sediment could disturb ~1.35 m$^2$ d$^{-1}$ and the sea star population at OAC could disturb ~75 m$^2$ and ~38 seeds (100% of recorded seeds) daily. Last, heart urchins observed in Shark Bay could disturb ~0.4 m$^2$ d$^{-1}$ at their highest densities recorded in this study; however, at higher

observed densities of 2–4 ind. m⁻² (J. Statton pers. obs.), urchins could disturb ~3 m² d⁻¹. If 50 m² restoration plots at OAC in Cockburn Sound or UL1 in Shark Bay were broadcast with 100 seeds m⁻², sand dollars could disturb 600–1600 seeds daily (12–32% of the seeds in the 50 m² plot), sea stars could disturb 7500 seeds daily (100% of the seeds in the 50 m² plot), and heart urchins could disturb 40–300 seeds daily (0.8–6% of the seeds in the 50 m² plot).

## Field bioturbator experiments

### Recently settled seeds

The 3 species of bioturbators exhibited different movement characteristics, affecting how they disturbed seeds on the surface versus seeds buried within the sediment. All 3 species of sediment bioturbators examined were capable of dislodging recently settled seeds in both Cockburn Sound and Shark Bay. The odds of a seed being disturbed were significantly higher in lanes with fauna present, i.e. sand dollars (odds ratio [OR]: 50.4, 95% CI: 8.8–290, p < 0.001), sea stars (OR: 170, 95% CI: 14–2100, p < 0.001), and heart urchins (OR: 9.2, 95% CI: 2.3–38, p = 0.001), than in their respective control lanes where animals were absent. Burial of seeds within lanes provided some refuge from disturbance, but the odds of buried seeds being disturbed in lanes with sand dollars (OR: 26, 95% CI: 3.1–220, p < 0.001), sea stars (OR: 8.9, 95% CI: 1.0–78, p = 0.05), and heart urchins (OR: 3.5, 95% CI: 4.7–330, p < 0.001) was still significantly higher than the odds of buried seeds being disturbed within control lanes.

The mean distance a seed moved on the surface was also significantly higher in lanes with sand dollars ($t_{7.2}$ = 9.5, p < 0.001), sea stars ($t_3$ = 5.2, p = 0.01), and heart urchins ($t_{9.9}$ = −2.6, p = 0.02) than in control lanes (Fig. 6, Table 2; Video 1 in the Supplement at www.int-res.com/articles/suppl/m595 p089_supp/). Burial of seeds again provided some refuge for seeds, as the mean distance seeds moved was significantly higher in lanes with sand dollars ($t_8$ = 3.1, p = 0.01) and heart urchins ($t_8$ = −3.2, p < 0.01) relative to control lanes (Table 2). Lanes containing sea stars did not show significantly higher movement of seeds than control lanes (p = 0.10). Sand dollar and sea star disturbance exclusively pushed seeds on the sediment surface or uprooted seeds initially
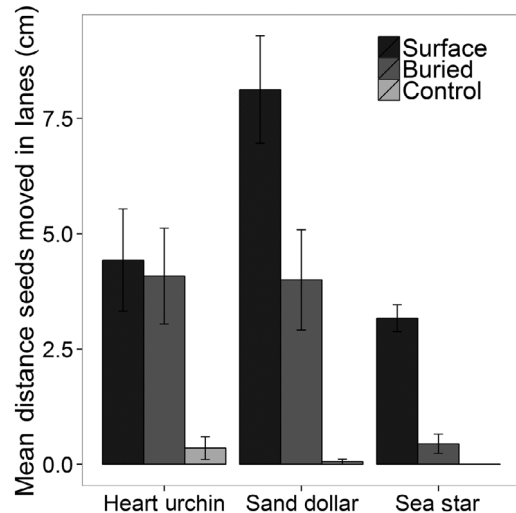


Fig. 6. Mean ± SE distance that *Posidonia australis* seeds moved in animal and control lanes (n = 9 lanes, each containing 3 seeds) for seeds on the surface or buried

buried 1 cm within the sediment. Interestingly, of the seeds initially buried, heart urchins dislodged 56% (n = 9), and pushed 44% (n = 7) beneath the sediment surface. Three seeds initially placed on the sediment surface were also found buried in urchin lanes.

The movement and disturbance of seeds placed within the path of animals outside experimental constructs was observed and demonstrated that animals disturbed seeds within their path equivalent to animals used within the experimental trials (Fig. S2).

### One year old seedlings

Both sand dollars and sea stars were unable to dislodge or move 1 yr old seedlings from the center of the lane; instead, they either moved around or stopped moving when they encountered a seedling. After each trial with an animal, seedlings were exca-

Table 2. Summary of *t*-tests evaluating differences in the mean movement of *Posidonia australis* seeds placed on the sediment surface or buried 2 cm in lanes with or without bioturbators

| Seed location | Bioturbator | Mean$_{with}$ | Mean$_{without}$ | t | df | p |
|---|---|---|---|---|---|---|
| Surface | Sand dollar | 8.1 | 0.1 | 9.5 | 7.2 | <0.001 |
| | Sea star | 3.2 | 0.0 | 5.2 | 3 | 0.01 |
| | Heart urchin | 5.0 | 0.6 | −2.6 | 9.9 | 0.02 |
| Buried | Sand dollar | 4.0 | 0.0 | 3.1 | 8 | 0.01 |
| | Sea star | 0.4 | 0.0 | 1.8 | 8 | 0.10 |
| | Heart urchin | 4.0 | 0.0 | −3.2 | 8 | 0.01 |

vated and we observed well established roots anchoring the seedlings in the sediment.

## DISCUSSION

We have demonstrated using field observations and field and laboratory experiments that sediment bioturbator communities in temperate and subtropical environments of Western Australia can dislodge recently settled seeds and act as a bottleneck to seedling establishment for a persistent and slow-growing seagrass species, *Posidonia australis*. The risk of bioturbators affecting 1 yr old seedlings, however, was minimal. These results suggest that if seeds can recruit and survive past the early stages of development, they may persist and contribute to meadow development, but only if other drivers of recruitment failure, whether they be biotic or abiotic, are absent or have been mitigated (Statton et al. 2017).

### Co-occurrence of sediment bioturbators and seeds

Bioturbators are common in soft sediments around the world (Kristensen et al. 2012) and have been well documented in, and adjacent to, seagrass meadows. The impact of their presence on seed and seedling recruitment will be a function of the abundance, location, and behavior of each bioturbator species (Valdemarsen et al. 2011, Delefosse & Kristensen 2012, Blackburn & Orth 2013, Statton et al. 2017). Our *in situ* surveys and experimental observations found that bioturbating species in unvegetated areas adjacent to seagrass meadows in Western Australia overlapped in space and time with recently released *P. australis* seeds and showed the potential for a negative relationship between the abundance of certain bioturbators and seed presence.

These observations and experiments support previous research suggesting that high densities of bioturbators will disturb recently settled seeds recruiting into degraded or unvegetated sediment habitats, and demonstrate that the mechanisms of disturbance can be diverse. The feeding and defecation of burrowing sediment detritivores, such as the polychaetes *Nereis diversicolor* and *Arenicola marina*, have buried seeds and seedlings of *Zostera noltii* and *Z. marina* below their critical depth for survival. This burial has been implicated as a major process that has slowed the recovery of both species (Philippart 1994, Hughes et al. 2000, Valdemarsen et al. 2011). A similar burrowing worm on the south coast of

Australia has damaged *P. australis* transplants in bare sediment, and would likely bury any seeds or seedlings in their vicinity (Bastyan & Cambridge 2008). Similarly, thalassinid shrimp burrowing in search of food and shelter have prevented seedling establishment of *Z. japonica* in bare sediment recently released from aquaculture production in the US Pacific Northwest (Dumbauld & Wyllie-Echeverria 2003). For these bioturbators, the relative impact of the bioturbator community on seedling recruitment stems from the density of bioturbators feeding or defecating in the vicinity of seeds, as mortality is caused by seed or seedling smothering adjacent to animal burrows. This study demonstrates a new group of echinoderm bioturbator species which act like bulldozers scraping either at the surface or subsurface sediments and uprooting recently settled seeds in their path. For this community, the impact of the bioturbators stems from both the density and mobility of the species present and pushing seeds around or out of the sediment where seeds are exposed to seed predators and further disturbance (Orth et al. 2002, 2006d, 2007). Because these echinoderm bioturbators are mobile, they may encounter multiple seeds or even the same seed on multiple occasions in a given day while foraging. These findings suggest the mechanism of seed disturbance will vary between bioturbator communities, largely based on the mobility and behavior of the species present.

Seed dormancy and germination traits will also be critical to understanding seedling establishment patterns in the presence of bioturbators. *P. australis* produces viviparous seeds with no dormancy (Orth et al. 2000) and a short window for seed settlement and establishment (Statton et al. 2017). Because mobile echinoderm bioturbators are not only capable of pushing seeds settled on the sediment surface but also of pushing seeds out of the sediment and back to the sediment surface, their activity at high densities may keep seeds on the surface without roots anchoring them in the sediment during periods of rapid leaf growth. This persistent disturbance of large and germinated *P. australis* seeds on the sediment surface may ultimately prevent incorporation in the sediment and the development of sufficient anchors to prevent growing seeds from floating away to unsuitable habitats. Our results demonstrating the consequences of bioturbator disturbance, in combination with the impacts of insufficient seed anchoring, may thus explain the low survival of seeded plots in sheltered locations with abundant bioturbator communities (Statton et al. 2017). Alternatively, seagrass species with seeds that have some form of dormancy, e.g.

*Zostera* spp. (Orth et al. 2000), may initially survive secondary dispersal events as a result of bioturbation, but ultimately may suffer similar fates to species with no dormancy, depending on their physical location within the sediment when they do germinate. The relative impact of incidental bioturbator disturbance will thus likely be larger in the short term for seeds without a dormancy period than for dormant seeds which may survive several disturbance events, and for whom survival will be dictated over a longer period of time. Seeds with dormancy may, however, encounter additional predation pressure over the length of their dormancy period that also reduces the number of viable seeds in the seed bank, and leads to lower seedling establishment rates.

The bioturbators studied here are a small subset of the global and diverse bioturbating community capable of disturbing seeds and/or seedlings. Larger bioturbators may also disturb the sediment when they forage for infauna. The green crab *Carcinus maenas* disrupted and uprooted *Z. marina* transplants in New England, USA (Davis et al. 1998). The portunid crab *Callinectes sapidus* is a known bioturbator of *Z. marina* meadows in the Atlantic (Wilson et al. 1990), and a relative, *Portunus armatus*, is a common bioturbator in Western Australia and was observed disturbing bare sediment during this study (Fig. S3). Likewise, elasmobranches are known to dig into both bare and vegetated patches in search of food and generate large pits in the sediment (Orth 1975, Townsend & Fonseca 1998). Previous studies have indicated that these elasmobranch bioturbators may (Orth 1975, Backman 1984, Fonseca et al. 1994, Inglis 2000) or may not (Valentine et al. 1994) be able to disturb adult clones of seagrass species, but these studies did not incorporate seeds and seedlings, which would be more susceptible to damage and loss from elasmobranch foraging. The widespread and diverse nature of bioturbators suggests these communities may play a more substantial role in seagrass seedling recruitment than currently acknowledged.

## Bioturbator movement and burial refuge

The impact that different bioturbator species will have on seed settlement and seedling establishment will be a direct function of the magnitude and frequency of sediment disturbance. The former effect will be a function of the size of the bioturbator species and the location of its movement in the sediment horizon. The latter effect will likely depend on the density or actual mobility of the bioturbator species.

For example, observations of sand dollars foraging through sediment indicate that sand dollars in this and previous studies will disturb the upper 1–2 cm of a 50 m$^2$ area every 3–8 d at conservative densities (~1 ind. m$^{-2}$, this study and Yeo et al. 2013) and daily at high densities (6 ind. m$^{-2}$, Forehead & Thompson 2010). These observations, combined with experimental results showing seed displacement, suggest that sand dollars exhibit a remarkable ability to disturb the sediment and dislodge or disrupt seeds on the sediment surface or shallowly buried in the sediment. In contrast, sea stars moved at a faster rate and covered greater areas but disturbed less of the sediment profile than did sand dollars and heart urchins. At their highest recorded densities, sea stars would move over the entire surface 4 times faster than sand dollars. At this level of activity, sea stars would frequently encounter seeds on the surface, but, should the seeds become buried, the seeds would largely escape the potential for sea star disturbance. During mating or stress behavior, however, sea stars regularly bury themselves in the upper 2 cm (Keesing et al. 2011, Lawrence et al. 2011). This behavior could move, overturn, or even bury recently settled seeds. Because *Archaster angulatus* (the sea star observed in Cockburn Sound) breeds en masse in late spring and early summer concurrent with *P. australis* seed release, the potential for this behavior to influence seed disturbance is substantial. The potential for seed disturbance from sea stars may thus stem not from the rate of movement, but rather from movement associated with mating activity in the vicinity of recently settled *P. australis* seeds.

Although much slower than sea stars and sand dollars, heart urchins were buried entirely within the sediment as they moved, and thus demonstrated more sediment turnover and seed disturbance. The heart urchins ploughed through the upper 4 cm of sediment, pushed seeds through the sediment, unearthed seeds from the sediment, and even buried seeds originally on the surface, demonstrating a distinct capacity to disturb seeds. Estimates of urchin density and movement in this study indicate that urchins will take substantially longer to disturb the same equivalent area as sand dollars or sea stars, but the impact of their movement on seeds on the surface or buried will be more substantial. Interestingly, related Spatangoida urchins have been reported to burrow deeper (5–15 cm) and move between 0.03 and 0.1 m d$^{-1}$ (Buchanan 1966, Lohrer et al. 2005), suggesting urchin species could be even more disruptive to seedling recruitment than recorded in this study.

## Implications of a potential seedling recruitment bottleneck from bioturbators

Here, we found that bioturbator disturbance from 3 echinoderm detritivores can be a significant potential bottleneck to *P. australis* seedling establishment and successful seedling recruitment. For clonal seagrass species, seedling establishment is most likely to occur in unvegetated or sparsely vegetated sediment areas (Orth et al. 2006a) that are, in many locations around the world, also habitat to a diverse array of sediment bioturbators. Other phalanx seagrass species may experience a similar bottleneck, as seedling recruitment is likely highest away from adult clones and within unvegetated sediments where bioturbators are most likely to have their greatest influence. In these areas, the high abundance and mobility of benthic fauna that are obligate bioturbators of bare substrate are a threat to newly settled seagrass seeds and therefore seagrass recovery via seedling recruitment. Diebacks of seagrass populations also generate bare sediment available for seedling recruitment (Orth et al. 2006c) and bioturbator foraging grounds. Bioturbator disturbance of seeds may thus slow the natural recovery of seagrass populations into these denuded areas. The variability of the bioturbator community captured in this study suggests that the effect of these animals on seedling survival will vary in space and may be stronger in locations with bioturbators impacting deeper portions of the sediment. Because seeds provide seagrass populations with important opportunities to disperse and to recover from disturbance (Jarvis & Moore 2010, Kendrick et al. 2012, 2017, Jarvis et al. 2014), incorporating the potentially additive effects of sediment bioturbator disturbance to seedling mortality may be important in predicting the distribution, stability, and recovery of seagrass populations. In addition, bioturbators impact both seed- and transplant-based restoration (Davis et al. 1998) and should be incorporated in future restoration planning. A diverse and global community of bioturbators may thus impact seed settlement and seedling survival for seagrass species with diverse life histories in both natural and restoration settings.

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