

Assessing methods for restoring seagrass (*Zostera muelleri*) in Australia's subtropical waters

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Abstract. *Zostera muelleri*, the dominant seagrass species along the eastern coastline of Australia, has declined due to anthropogenic stressors, including reduced water clarity. Water quality has improved in recent years, but restoration efforts are hampered by limited knowledge of transplantation methods. To support future restoration efforts, we tested multiple techniques for transplanting mature seagrass shoots: (1) sediment cores with intact seagrass plants (plug); (2) individual shoots anchored on frames (frame); (3) frame methods combined with subsurface mats to exclude bioturbating animals (mat + frame); (4) above-ground cages to exclude grazing fish (cage + frame); and (5) combined treatment of above-ground cages and subsurface mats (cage + mat + frame). Transplant success over 10 months showed considerable variability among locations. At one site, seagrass persisted in all treatments, with highest growth in the mat + frame treatment. At two locations, uncaged shoots were lost within 6–35 days of transplanting, presumably due to grazing by fish. In treatments with cages, growth was again highest in the mat + frame treatment. At the fourth location, all seagrass was lost due to physical stress. Thus, we conclude that transplantation success is highest using the mat + frame technique, but overall success depends on careful assessment of biotic and abiotic stressors at the chosen locations.

Additional keywords: bioturbation, grazing, method assessment, restoration.

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Introduction

Seagrasses form very productive coastal ecosystems with high biodiversity that drives important biogeochemical and ecological functions (van Katwijk *et al.* 2016; Nordlund *et al.* 2018). They provide essential ecosystem services, such as carbon sequestration (Duarte *et al.* 2010; McLeod *et al.* 2011), nutrient uptake (Flindt *et al.* 1999; Lillebø *et al.* 2004) and biodiversity conservation (Sievers *et al.* 2019; Unsworth *et al.* 2019). However, seagrass coverage has declined worldwide (e.g. Waycott *et al.* 2009). Ongoing declines have been linked directly to human-induced stressors that reduce the extent of habitats suitable for seagrass growth, often through changes in water and sediment quality, reduced light penetration and direct removal (e.g. dredging) among others (Short *et al.* 2007; Moksnes *et al.* 2008; Kendrick *et al.* 2017). Loss of key ecosystem engineers, like seagrass, alters the physical structure and functionality of coastal environments (Flindt *et al.* 2016), leading to unvegetated areas dominated by large bioturbators, such as lugworms (*Arenicola marina*) or callianassid shrimp (*Trypaea australiensis*; Valdemarsen *et al.* 2011; Eklöf *et al.* 2015).

Natural recovery of seagrass habitats is generally low due to the vulnerability of seeds and seedlings to physical disturbances

and biological stressors (Flindt *et al.* 2016; Kuusemäe *et al.* 2016; Smith *et al.* 2016). For *Zostera* spp., high seedling mortality is often caused by physical stress from sediment resuspension and drifting algae (Rasheed 2004; Orth *et al.* 2006; Valdemarsen *et al.* 2010). Direct consumption by large herbivores, such as sea turtles, dugong and fish in the tropics (Aragones and Marsh 1999; Valentine *et al.* 2006; Goldenberg and Erzini 2014) and swans in temperate regions (Dos Santos *et al.* 2013), can also reduce natural recovery.

Seagrass restoration has been attempted worldwide to mitigate the widespread loss of seagrass habitats. Successful restoration depends on several factors, such as appropriate choice of transplantation site, size of transplantation area and transplantation methods (van Katwijk *et al.* 2016). Accordingly, transplantation techniques and locations should be tested under local conditions before large-scale transplantation efforts are undertaken (van Katwijk *et al.* 2016). Both shoots and seeds have been used in previous restoration efforts, with variable success (van Katwijk *et al.* 2016). For example, *Zostera muelleri* shoots were successfully transplanted in New Zealand (Matheson *et al.* 2017), but similar techniques failed in Australia (McLennan and Sumpton 2005). Similarly,

Zostera marina seeds were used to successfully restore seagrass meadows in Chesapeake Bay, USA (Orth *et al.* 2012), whereas seed restoration in north-west Sweden remained unsuccessful (Eriander *et al.* 2016).

The seagrass *Z. muelleri* is the dominant species in estuaries and bays along the east coast of Australia (Short *et al.* 2010), but it has declined markedly in urbanised locations in recent decades due to dredging, coastal development and urban and agricultural run-off (Walker and McComb 1992; Waycott *et al.* 2009; Dunn *et al.* 2014; Maxwell *et al.* 2017). Several protection and mitigation measures have been implemented in Australia to combat declines in important habitats, including seagrasses (Natura Pacific 2012; Seagrass-Watch 2015). Of particular note are requirements for developers to offset losses (Australian Wetlands 2009), generally through restoration or transplant activities. Understanding techniques that optimise the success of these offset activities will benefit the long-term conservation of these important habitats.

The Gold Coast is a city in Queensland, Australia, situated around extensive tidal waterways and estuaries with freshwater input from several rivers (Dunn *et al.* 2014). The city has undergone rapid expansion in both population and urbanised area in recent decades. As a consequence, many marine ecosystems are threatened by urban developments. For example, ~10 000 m² of seagrass was removed from the city's primary embayment, the Broadwater in southern Moreton Bay, for a single urban project (VDM Consulting 2012). As a result, the existing *Z. muelleri* meadows have become increasingly fragmented (Waycott *et al.* 2009), suggesting an urgent need for restoration actions.

Restoration of *Z. muelleri* has generally had low success in Australian waters, suggesting that this species is either unsuitable for restoration or that more appropriate restoration methods are needed (York and Smith 2013). However, Matheson *et al.* (2017) tested various techniques for *Z. muelleri* restoration in New Zealand and reported an increase of up to 63% in seagrass coverage when using plugs and sods. Therefore, restoration of this species is possible under suitable environmental conditions when using appropriate techniques.

The aim of this study was to test methods for *Z. muelleri* restoration and to identify potential stressors in the subtropical waters of Queensland. Various transplantation techniques were used in two shallow estuaries. The effects of specific stressors were evaluated using exclusion treatments. The transplanted areas were subsequently monitored closely, and the fate of transplanted shoots was related to the prevailing physical, chemical and biological conditions.

Materials and methods

Transplantation locations

Seagrass (*Z. muelleri*) transplantation was performed at four locations in the Gold Coast Broadwater and Tallebudgera Creek, ~15 km south of the Broadwater (Fig. 1). There were two transplantation locations in the Broadwater (Broadwater exposed, BE; and Broadwater sheltered, BS) and two in Tallebudgera Creek (Tallebudgera upper, TU; and Tallebudgera lower, TL). All locations were subtidal and close to highly urbanised areas.

The Broadwater is an estuary extending northward from Southport to Moreton Bay. It is separated from the ocean by barrier islands and has two openings to the South Pacific Ocean. All locations in the Broadwater are mesotidal with maximum tidal amplitudes of 2 m and a mean salinity of ~33 (Dunn *et al.* 2014). The Broadwater is influenced by freshwater input from four major rivers (Mirfenderesk and Tomlinson 2008). High boating activity is a potential disturbance within the Broadwater through increased wave energy, shading and anchoring.

Tallebudgera Creek originates in the Springbrook National Park and has a length of 25 km, including several man-made canals, and flows directly into the Coral Sea of the South Pacific Ocean at Burleigh Heads. The Tallebudgera Creek locations in this study have a tidal range of ~1.8 m (Abdullah and Lee 2016) and experience variable salinity from 29 to 36 at TU (Morton 1992; dictated by tidal state and recent rainfall).

Shoot transplantation

Transplant experiments began in February 2016 and were monitored by counting the total number of shoots at each treatment daily to weekly for the first 6 weeks and then monthly thereafter until December 2016. Shoots for transplantation were collected from donor meadows less than 30 m from transplantation sites and at the same depth as the transplant site. The following combinations of transplant techniques (treatments) were used (Fig. 2).

1. Plug ($n = 5$ at each site, except TU): intact seagrass shoots with undisturbed rhizosphere, rhizomes and roots were taken from the donor meadow in 15-cm diameter cores and a depth of ~15 cm. The shoots were deployed by extruding the plug before burial into the sediment at the transplantation site while ensuring that the rhizomes and base of the shoots were level with the surrounding sediment surface. The plug approach has been successfully used in several studies (e.g. Fonseca *et al.* 1998).
2. Frame ($n = 5$ at each site): iron frames (32 × 32 cm; mesh size 16 × 16 cm) were used to anchor 16 individual shoots mounted with cable ties (equalling ~0.1024 m² and a density of 156 shoots m⁻²). Only mature and intact shoots without side branches and with a rhizome length of at least 4 cm were transplanted. The cable tie was fixed to the rhizome behind the first internode. The frames were carefully deployed in the upper sediment layer with all shoots pointing upwards.
3. Mat + frame ($n = 5$ at each site): the mat + frame approach was used to avoid effects from bioturbation by placing frames on top of buried mats. A protective 60 × 60-cm mat made from 1-mm double-layer hessian with a mesh size of 2 mm was buried 5 cm into the sediment before placing a frame with shoots mounted as described above for the frame treatment.
4. Cage + frame ($n = 5$, only at TU): the cage + frame approach was used to prevent grazing by fish and other large herbivores. Frames prepared as described above for the frame treatment were protected by a fully enclosed net cage (38 cm wide × 60 cm long × 29 cm high) with a 2-cm mesh and open towards the bottom. The large mesh size allowed sufficient light penetration for seagrass growth and did not alter currents.

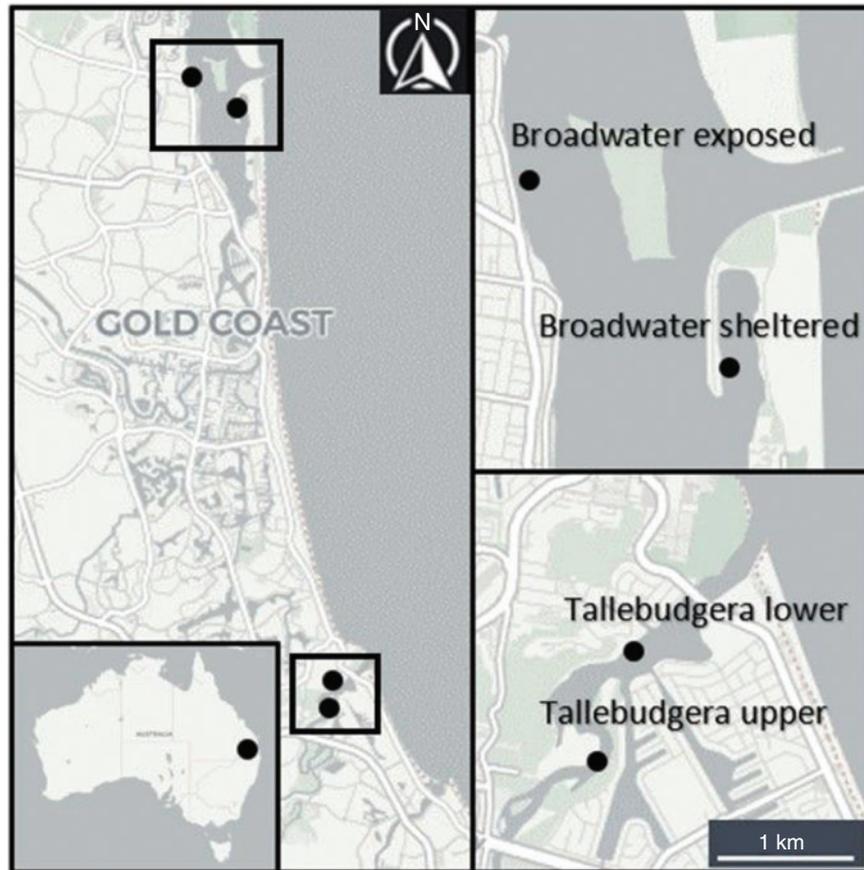


Fig. 1. Site of the four experimental transplantation sites in south-east Queensland, Australia. BE, Broadwater exposed (27.93557°S, 153.40776°E); BS, Broadwater sheltered (27.94748°S, 153.42236°E); TU, Tallebudgera upper (28.10984°S, 153.44888°E); TL, Tallebudgera lower (28.10197°S, 153.45150°E).

5. Cage + mat + frame ($n = 4$, only at TU): the cage + mat + frame approach combined the treatment preparation and exclusion methods of mat + frame and cage + frame to exclude both bioturbation and grazing.

It should be emphasised that no plug treatment was used at TU and that this was the only location with cage treatments. All shoots used in the plug treatments and those mounted on frames were handpicked directly from the donor seagrass meadows and transplanted within 4 h. Transplantations were always performed in three transects parallel to the nearest shore line, with 2 m between the individual treatments, which were placed in randomised order.

Sediment characteristics

Sediments at each transplantation site were assessed to infer site suitability and local hydrodynamic regimes. Sediments dominated by coarser grain sizes, and with low organic content, for example, may indicate high levels of exposure to hydrodynamic forcing (Fonseca *et al.* 1983). Surface sediments were sampled with cores (inner diameter 5 cm) at each donor and transplant site ($n = 4$) and the upper 1 cm of sediment was analysed. Sediment water content was determined gravimetrically as

weight loss after drying at 105°C for 24 h. Organic carbon content was analysed on dried sediment subsamples using an elemental analyser (Flash EA 2000 Series; Thermo Analytical; ThermoFisher Scientific, Bremen, Germany) after acidification with HCl fumes to remove inorganic carbon. Grain size distribution was analysed on a Malvern Master sizer 3000 (Malvern Instruments Ltd, Malvern, UK).

*Characteristics of *Z. muelleri* donor plants*

Fresh *Z. muelleri* shoots were randomly harvested from the donor meadows ($n = 10$). The sampled plants were separated into above- (A) and below-ground (B) biomass and the A : B ratio was calculated based on the dry weight (105°C, 24 h). The presence of epiphyte coverage was identified visually.

Yabby exclusion with mats

Densities of the dominant bioturbating species, namely the Australian ghost shrimp, or 'yabby', *T. australiensis*, were assessed at each transplantation site by counting burrow openings within six randomly placed frames (diameter 41 cm, area 0.13 m²) nearby transplant plots. The abundance of yabbies was estimated by dividing the total number of burrow openings by

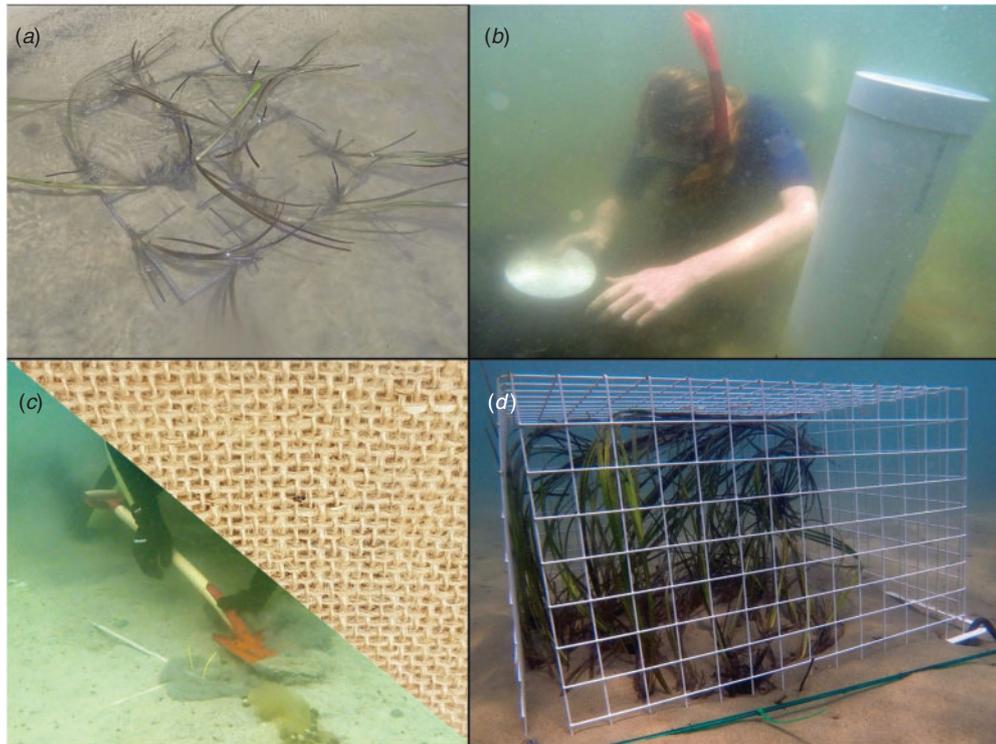


Fig. 2. The different transplantation methods used in this study: (a) frame; (b) plugs; (c) mat; and (d) cage. Photographs taken by Troels Lange and Nele Svenja Wendländer.

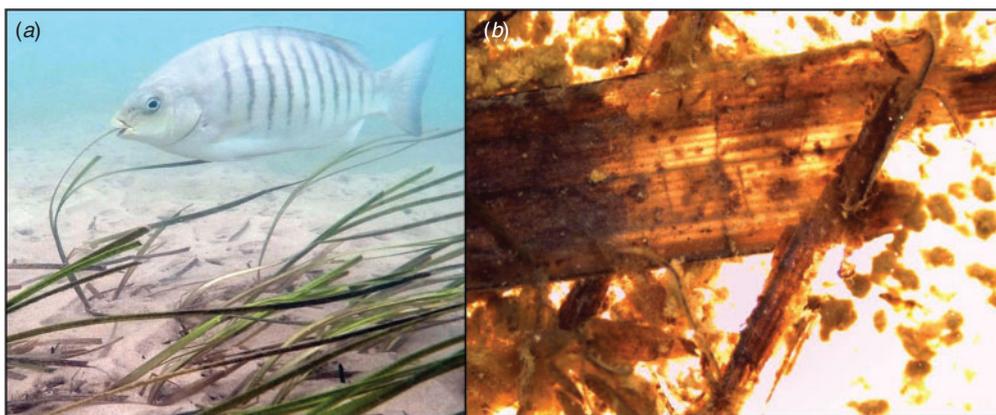


Fig. 3. (a) Luderick (*Girella tricuspidata*) grazing on transplanted *Zostera muelleri*. (b) Stomach contents of a Luderick from Tallebudgera upper. Photographs taken by Troels Lange and Erik Kristensen.

2.1 (Butler and Bird 2007). The efficacy of buried hessian mats to exclude yabbies was tested by placing mats ($n = 5$) in an unvegetated area at TU with a high density of yabbies. The mats were similar to those in the transplanted area and were buried to the same depth. The abundance of burrow openings above the mats was monitored over a 6-week period.

Effects of mobile fauna

Test transplantations conducted at TU before the main transplantation experiment revealed that the leaves on all shoots were

rapidly grazed to a height of only 2–4 cm within the first 24 h. For further clarification, cameras were installed at all transplantation locations for short-interval time-lapse photography (twice over a period of 6 h at 5-s intervals). The fish species *Girella tricuspidata* (Luderick) was captured by camera and identified as a potential grazer (Fig. 3). Stomach contents of Luderick specimens ($n = 3$) caught over adjacent meadows at TU were used to confirm this grazing behaviour (Fig. 3). Thus, the experimental design was altered at TU to exclude Luderick using cages over transplant plots.

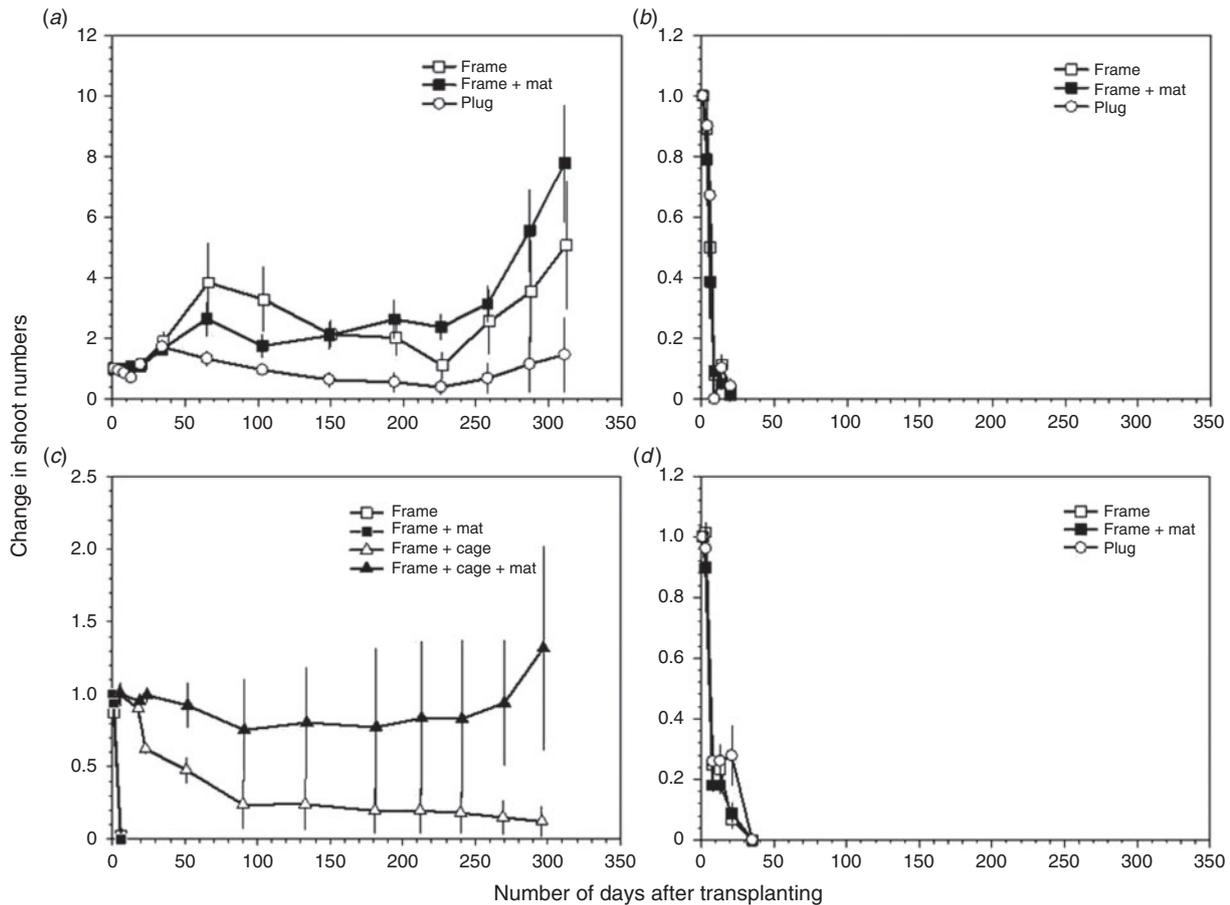


Fig. 4. Changes in shoot numbers relative to an initial value of 1 for the different transplantation methods used at the four transplant locations: (a) Broadwater sheltered; (b) Broadwater exposed; (c) Tallebudgera upper; and (d) Tallebudgera lower. Data are the mean \pm s.e.

Statistical analysis

Data from the 10-month monitoring were analysed as a function of time by a general repeated-measures linear model, with change in shoot numbers for all treatments of transplanted shoots and yabby density as dependent variables (two-way analysis of variance (ANOVA) and Tukey *post hoc* test). The success of the various treatments was compared for the full monitoring period. Short-term (<2 months; change in shoot numbers for all treatments of transplanted shoots and yabby density) or data from one time point (e.g. sediment characteristics) were analysed by one-way ANOVA. The level of significance was set at $P < 0.05$.

Results

Transplantation outcome

The fate of transplanted *Z. muelleri* shoots varied considerably among locations and treatments. All transplanted shoots at BE and TL were lost within 20 and 35 days respectively, regardless of transplant technique (Fig. 4). At TU, uncaged treatments disappeared within 7 days, whereas caged treatments survived considerably longer. However, only treatments that were further protected by subsurface mats remained stable, showing a marginal but non-significant increase in the number of shoots over

time ($P > 0.05$). Nevertheless, this treatment had significantly higher shoot density at the end of the experiment than treatments without mat protection ($P < 0.05$).

Transplants at BS, particularly those using frames (with or without a protective mat), were the most successful. For example, transplants using the frame + mat treatment increased in shoot number by a mean (\pm s.e.) of $678 \pm 94\%$ over the 300-day monitoring period. No significant differences were found between frame treatments with or without mats, but both treatments had significantly higher number of shoots than the plug treatment ($P < 0.05$) at the end of the monitoring period. However, shoot abundance in the plug treatments was still a mean (\pm s.e.) of $46 \pm 23\%$ higher at the end of the monitoring period than initially transplanted.

Sediment characteristics

The sediment conditions differed considerably among the four selected locations and between donor and transplantation sites (Table 1). All donor sites except for BS had significantly higher ($P < 0.05$) water, organic carbon and silt + clay content (and thus smaller median grain size) than the transplant sites (Table 1). The Tallebudgera donor locations (TU and TL) were significantly richer ($P < 0.05$) in organic content and silt + clay

Table 1. Characteristics of seagrass and sediment (sediment water content, organic content and grain size) at donor and bare bottom (transplantation sites)

The above- to below-ground biomass (A : B) ratios of *Zostera muelleri* at donor locations and yabby abundance at transplant locations are also shown. Data are the mean \pm s.d. ($n = 4$ for sediment cores; for yabby abundance, $n = 13$ at Tallebudgera upper, TU; $n = 12$ at Broadwater sheltered, BS; $n = 5$ at Tallebudgera lower, TL; and $n = 3$ at Broadwater exposed, BE)

Site		Water content (%)	Organic carbon (%)	Silt + clay content (%)	Median grain size (mm)	A : B ratio	Yabby abundance (individuals m ⁻²)
TU	Donor	49 \pm 2	1.64 \pm 0.31	28.1 \pm 6.0	0.16 \pm 0.02	1.4 \pm 0.4	
	Transplant	25 \pm 2	0.56 \pm 0.43	7.4 \pm 2.7	0.26 \pm 0.01		96.4 \pm 6.9
TL	Donor	34 \pm 12	0.85 \pm 0.72	14.1 \pm 8.2	0.24 \pm 0.02	1.2 \pm 0.3	
	Transplant	22 \pm 1	0.11 \pm 0.03	3.5 \pm 0.3	0.27 \pm 0.00		3.8 \pm 1.3
BS	Donor	22 \pm 1	0.16 \pm 0.05	4.6 \pm 1.2	0.28 \pm 0.01	0.7 \pm 0.3	
	Transplant	22 \pm 1	0.12 \pm 0.02	3.5 \pm 0.5	0.28 \pm 0.01		7.4 \pm 2.2
BE	Donor	26 \pm 1	0.22 \pm 0.18	2.5 \pm 0.4	0.18 \pm 0.00	1.0 \pm 0.4	
	Transplant	19 \pm 1	0.04 \pm 0.01	0.00 \pm 0.01	0.25 \pm 0.01		1.0 \pm 1.0

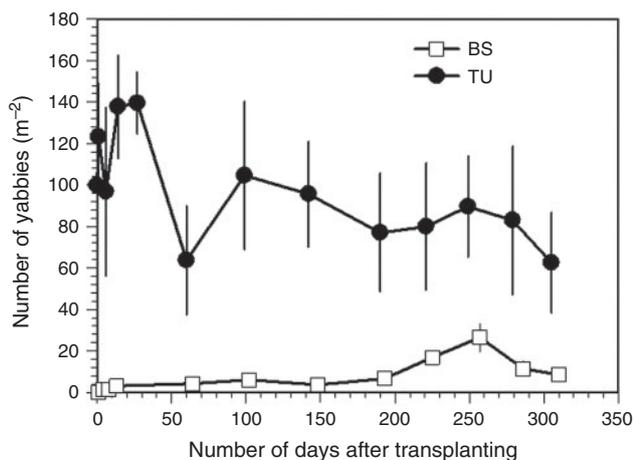


Fig. 5. Density of callinassid shrimp (yabbies) over the course of the experiments at the two locations where seagrass persisted, namely Broadwater sheltered (BS) and Tallebudgera upper (TU). Data are the mean \pm s.e. ($n = 6$).

content than those in the Broadwater (BS and BE), whereas no such location-specific pattern was evident for median grain size. However, there was no significant difference in median grain size among transplant locations, but organic and silt + clay content was significantly higher at TU than BE, with TL and BS having intermediate levels. It should be noted that the BE transplant sediment was remarkably low in organic content and contained no silt + clay.

Characteristics of donor seagrass

The A : B ratios of *Z. muelleri* from the donor locations were highest at TU and lowest at BS, but only differed significantly between TU and BS, and between TL and BS (Table 1). No epiphytes were present on *Z. muelleri* leaves at TL and BS, whereas leaves at TU and BE were densely covered with epiphytes. It is noteworthy that *Z. muelleri* morphology varied among locations: mature *Z. muelleri* shoots at BS were quite short and delicate with a morphology similar to seedlings from the other locations.

Abundance of yabbies

Yabbies (*T. australiensis*) were mainly present in non-vegetated sediment at transplant sites. The abundance of yabbies varied considerably among locations, with significant 10- to 100-fold higher counts at TU than at BS, TL and BE (Table 1). The yabby populations remained similar over the 300-day monitoring period at TU and BS (Fig. 5). No signs of yabby burrow openings were evident on the sediment surface of areas where hessian mats were buried, indicating that these mats were an effective yabby exclusion method.

Mobile fauna

Time-lapse photographs from the transplanted *Z. muelleri* in the Tallebudgera estuary frequently captured luderick (*G. tricuspidata*) grazing on leaves of the transplanted shoots at both TU and TL (Fig. 3). Luderick were also observed at BE, but never actively grazing on *Z. muelleri* leaves. No luderick were spotted at BS. The stomach content of all the three luderick examined from TU contained large amounts of identifiable remains of *Z. muelleri* leaves (Fig. 3).

Discussion

The significant variations in the growth and survival of *Z. muelleri* transplants among the Gold Coast locations examined indicate differences in site-specific stressors. The transplantation methods and protective approaches used also had vastly different effects on *Z. muelleri* survival both within and among locations. Therefore, the results indicate that the approach used for successful transplantation is highly site specific, and that a closer examination of local physical and biological conditions with appropriate tests is required at each site before initiating large-scale transplantation efforts, as described in other studies (Connolly *et al.* 2016; van Katwijk *et al.* 2016). Use of a hydrodynamic-based ecological modelling approach, where the different stressors are included, will support selection of optimal restoration sites (Kuusemäe *et al.* 2016, 2018).

Both anchoring shoots to objects (e.g. iron frames, stones, shells) and transplanting sediment plugs with shoots and rhizomes intact are commonly used techniques for seagrass

restoration. In the present study the use of iron frames was more successful than the use of plugs. It is unclear why the plug treatment can be used successfully for *Z. muelleri* transplantations in New Zealand (Matheson *et al.* 2017) whereas this method is less effective in Australian locations. Eriander *et al.* (2016) had similar experience when comparing transplantation of individual *Z. marina* shoots with and without plugs, finding that the plug method was ineffective with a 2-month lag phase and an overall 3.5-fold lower increase in shoot numbers over 14 months compared with individual unanchored transplants. It is possible that the shoots within plugs are unable to expand their roots and rhizomes from the original sediment into the new substratum at the transplantation site. Further research is required to elucidate the physical, chemical or biological causes for this phenomenon.

Successful seagrass restoration is clearly dependent on the choice of transplantation technique, but it also requires a suitable transplantation site without excessive stressor impact (van Katwijk *et al.* 2016). Even sites next to existing seagrass meadows may be unsuitable for restoration. The dense vegetation creates self-protection against physical and biological stressors and supports continuous growth within the boundaries of existing meadows (Suchanek 1983; Berkenbusch *et al.* 2007), but with slow meadow expansion (N. S. Wendländer, pers. obs.). However, restored areas with open vegetation cover of transplanted shoots are vulnerable due to lack of self-protection (van der Heide *et al.* 2007; Maxwell *et al.* 2017).

The Gold Coast locations studied here have different exposures to physical stress, particularly in the form of current velocity and wave energy. The sediment analysis suggests differences that support these observations. The highest physical exposure occurs at location BE, which is supported by our analyses that show lower small particle content (silt + clay) at sites with strongest hydrodynamics (Table 1). The high physical stress at BE may have been the main cause for the rapid loss of transplanted shoots due to sediment erosion and uprooting (Fig. 4). Conversely, BS was apparently sufficiently protected with low current velocities (Mirfenderesk and Tomlinson 2008) and wave energy to allow the survival and growth of transplanted shoots, leading to rapidly emerging transplantation patches. This high success indicates that areas with low physical energy, as at this location (BS), may be best suited for future restoration efforts.

It is feasible that seagrasses in Tallebudgera Creek are generally exposed to poorer growth conditions than those in the Broadwater, particularly the BS location. At these sites, the light-demanding transplanted seagrass shoots may be hampered by lack of light due to high water turbidity from frequent resuspension events (Eriander *et al.* 2016; Flindt *et al.* 2016). Although no light measurements or water turbidity data are available, we observed higher A : B ratios in donor locations at TU than BS. This may indicate lower light availability at Tallebudgera than the Broadwater because seagrasses that grow under low light conditions invest more energy into longer leaves (Abal *et al.* 1994). At TU, for example, sediment is washed into the estuary after heavy rain events, leading to high turbidity and visibility of only a few centimetres for several days (N. S. Wendländer, pers. obs.). No such events were observed at BE and BS, suggesting a better light climate at these locations. The

high A : B ratio at Tallebudgera may also be due to low investment in root biomass at these locations with relatively low hydrodynamic stress and sufficient nutrients when compared to BE (York *et al.* 2013; Maxwell *et al.* 2017). Furthermore, the denser cover of epiphytes on seagrass leaves at TU than BS may contribute to light limitation at the former site (Nelson 2017).

Biological stressors can also play a role in transplant success (van Katwijk *et al.* 2016). Bioturbating fauna (e.g. yabbies) are defined as ecosystem engineers (i.e. van Wesenbeeck *et al.* 2007), by mobilising sediment and altering the living conditions for associated organisms. Some upward conveyor species, such as lugworm and yabbies (*T. australiensis*), intensely rework subsurface particles to the sediment surface (Cadée 1976; Kristensen *et al.* 2012). Although the dense rhizome network in a mature seagrass meadow hampers infaunal reworking (Eklöf *et al.* 2015), widely dispersed transplanted shoots lack this effect and are rapidly buried (Valdemarsen *et al.* 2010, 2011). Similarly, Valdemarsen *et al.* (2011) showed that even a low density of 5–10 individuals m⁻² of the intense reworker *A. marina* has a negative effect on seagrass abundance. The applicability of the mat technique and its protection capacity was evident at TU, where the yabby density was higher than at all other locations (10- to 100-fold higher). The mat treatment was also a successful transplant technique at BS, with a modest abundance of yabbies (7 individuals m⁻²), suggesting that transplant experiments are more likely to succeed in yabby-colonised areas if they include protective subsurface mats.

Transplanted shoot numbers at all treatments at TL declined rapidly within the first 35 days. Herbivory appears to be another important constraint in these transplant experiments. Camera observations and fish stomach content analyses from TU showed that luderick (*G. tricuspidata*), a herbivorous fish, directly consumes seagrass and was frequently present at all locations, except BS. Luderick were observed grazing the tips of seagrass leaves (Fig. 3). Accordingly, luderick could be considered a significant grazer of seagrass, which was confirmed by the high content of seagrass tissue in the stomach of examined luderick. The negative effect of luderick on transplanted shoots was indirectly confirmed by the cage treatments at TU. Uncaged transplants disappeared within 2 days, whereas caged shoots survived for at least 300 days. Luderick are widely distributed throughout eastern Australia (Atlas of Living Australia 2019), suggesting that this phenomenon may have a strong effect on the success of *Z. muelleri* restoration in Australia. The precise role of grazing by fish on seagrass survival deserves further research. We recommend that, at a minimum, areas selected for large-scale eelgrass transplantation should be surveyed for potential grazers. If grazers are present, tests are needed to determine whether it is necessary to apply grazing protection of the transplanted shoots and, if so, how feasible that is at scale.

Conclusions

The present study demonstrates that, provided the right restoration technique or combination of restoration techniques are used, seagrass restoration is possible in the subtropical waters of Queensland. This contradicts the current perception that seagrass restoration is not a recommended compensation measure

(York and Smith 2013). However, a few guidelines should be followed when restoration is planned to ensure success. The stressors at a potential restoration site must be identified and the restoration approach adjusted accordingly. It is recommended that test transplantations are performed at the selected locations before undertaking large-scale restoration actions. In general, strongly physically affected locations, such as BE, should be avoided. Because the selected locations should provide sufficient light, areas with high turbidity and nutrient levels supporting the growth of epiphytes should be avoided. Furthermore, intense infaunal reworking by, for example, yabbies should be avoided by selecting locations without these animals or by the placement of protective mats under the transplanted shoots. Due to the potential grazing pressure of, for example, luderick, restoration sites should be located in areas with a low abundance of this grazer or protection methods in the form of cages should be used if feasible. The best performance of transplanted seagrass with the highest increase in shoot numbers can be ensured by using the frame, mat + frame or cage + mat + frame techniques.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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References

- Abal, E. G., Loneragan, N., Bowen, P., Perry, C. J., Udy, J. W., and Dennison, W. C. (1994). Physiological and morphological responses of the seagrass *Zostera capricorni* Aschers. to light intensity. *Journal of Experimental Marine Biology and Ecology* **178**(1), 113–129. doi:10.1016/0022-0981(94)90228-3
- Abdullah, M. M., and Lee, S. Y. (2016). Meiofauna and crabs in mangroves and adjoining sandflats: is the interaction physical or trophic? *Journal of Experimental Marine Biology and Ecology* **479**, 69–75. doi:10.1016/J.JEMBE.2016.03.004
- Aragones, L., and Marsh, H. (1999). Impact of dugong grazing and turtle cropping on tropical seagrass communities. *Pacific Conservation Biology* **5**(4), 277–288. doi:10.1071/PC000277
- Atlas of Living Australia (2019). *Girella tricuspidata* (Quoy & Gaimard, 1824): Luderick. In 'Atlas of Living Australia'. (CSIRO: Canberra, ACT, Australia.) Available at <https://bie.ala.org.au/species/urn:lsid:biodiversity.org.au:afd.taxon:b9adeefd-97c6-4748-a1fe-489fbc7398b4> [Verified 30 October 2019].
- Australian Wetlands (2009). Southport Parklands redevelopment seagrass establishment report. Report for ABIGROUP Constructions Pty Ltd. Australian Wetlands Pty Ltd, Byron Bay, NSW, Australia.
- Berkenbusch, K., Rowden, A. A., and Myers, T. E. (2007). Interactions between seagrasses and burrowing ghost shrimps and their influence on infaunal assemblages. *Journal of Experimental Marine Biology and Ecology* **341**, 70–84. doi:10.1016/J.JEMBE.2006.10.026
- Butler, S., and Bird, F. (2007). Estimating density of intertidal ghost shrimps using counts of burrow openings. Is the method reliable? *Hydrobiologia* **589**, 303–314. doi:10.1007/S10750-007-0747-X
- Cadée, G. C. (1976). Sediment reworking by arenicola marina on tidal flats in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* **10**(4), 440–460. doi:10.1016/0077-7579(76)90020-X
- Connolly, R., Dunn, R., Flindt, M., Jackson, E., Kristensen, E., McKenna, S., Olds, A., Rasheed, M., Schlacher, T., and York, P. (2016). Assessment of the effects of foreshore nourishment and mitigation projects on seagrass ecosystems. Report to Gold Coast Waterways Authority, SRMP-004, Griffith University, Gold Coast, Qld, Australia.
- Consulting, V. D. M. (2012). Ecological investigations to support the Broadwater Masterplan. (Gold Coast City Council: Gold Coast, Qld, Australia.) Available at <https://www.goldcoast.qld.gov.au/ecological-investigations-to-support-the-broadwater-masterplan-18929.html> [Verified 31 October 2019].
- Dos Santos, V. M., Matheson, F. E., Pilditch, C. A., and Elger, A. (2013). Seagrass resilience to waterfowl grazing in a temperate estuary: a multi-site experimental study. *Journal of Experimental Marine Biology and Ecology* **446**, 194–201. doi:10.1016/J.JEMBE.2013.05.030
- Duarte, C., Marba, N., Gacia, E., Fourqurean, J., Beggins, J., Barrón, C., and Apostolaki, E. (2010). Seagrass community metabolism: assessing the carbon sink capacity of seagrass meadows. *Global Biogeochemical Cycles* **24**(4), GB4032. doi:10.1029/2010GB003793
- Dunn, R., Waltham, N., Benfer, N., King, B., Lemckert, C., and Zigic, S. (2014). Gold Coast Broadwater: Southern Moreton Bay, Southeast Queensland (Australia). In 'Estuaries of Australia in 2050 and Beyond'. (Ed. E. Wolanski.) pp. 93–109. (Springer: Dordrecht, Netherlands.)
- Eklöf, J. S., Donadi, S., van der Heide, T., van der Zee, E. M., and Eriksson, B. K. (2015). Effects of antagonistic ecosystem engineers on macrofauna communities in a patchy, intertidal mudflat landscape. *Journal of Sea Research* **97**, 56–65. doi:10.1016/J.SEARES.2014.12.003
- Eriander, L., Infantes, E., Olofsson, M., Olsen, J., and Moksnes, P.-O. (2016). Assessing methods for restoration of eelgrass (*Zostera marina* L.) in a cold temperate region. *Journal of Experimental Marine Biology and Ecology* **479**, 76–88. doi:10.1016/J.JEMBE.2016.03.005
- Flindt, M., Pardal, M., Lillebø, A. I., Martins, I., and Marques, J. (1999). Nutrient cycling and plant dynamics in estuaries: a brief review. *Acta Oecologica* **20**(4), 237–248. doi:10.1016/S1146-609X(99)00142-3
- Flindt, M., Rasmussen, E., Valdemarsen, T., Erichsen, A., Kaas, H., and Canal-Vergés, P. (2016). Using a GIS-tool to evaluate potential eelgrass reestablishment in estuaries. *Ecological Modelling* **338**, 122–134. doi:10.1016/J.ECOLMODEL.2016.07.005
- Fonseca, M. S., Zieman, J. C., Thayer, G. W., and Fisher, J. S. (1983). The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. *Estuarine, Coastal and Shelf Science* **17**, 367–380. doi:10.1016/0272-7714(83)90123-3
- Fonseca, M. F., Kennworthy, W. J., and Thayer, G. W. (1998). Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. National Oceanic and Atmospheric Administration (NOAA), Coastal Ocean Program Decision Analyses 12, NOAA, Washington, DC, USA.
- Goldenberg, S. U., and Erzini, K. (2014). Seagrass feeding choices and digestive strategies of the herbivorous fish *Sarpa salpa*. *Journal of Fish Biology* **84**(5), 1474–1489. doi:10.1111/JFB.12371
- Kendrick, G., Orth, R., Statton, J., Hovey, R., Ruiz Montoya, L., Lowe, R., Krauss, S., and Sinclair, E. (2017). Demographic and genetic connectivity: the role and consequences of reproduction, dispersal and recruitment in seagrasses. *Biological Reviews of the Cambridge Philosophical Society* **92**(2), 921–938. doi:10.1111/BRV.12261
- Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C. O., and Banta, G. T. (2012). What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series* **446**, 285–302. doi:10.3354/MEPS09506

- Kuusemäe, K., Rasmussen, E. K., Canal-Vergés, P., and Flindt, M. R. (2016). Modelling stressors on the eelgrass recovery process in two Danish estuaries. *Ecological Modelling* **333**, 11–42. doi:10.1016/J.ECOLMODEL.2016.04.008
- Kuusemäe, K., von Thenen, M., Lange, T., Rasmussen, E. K., Pothoff, M., Sousa, A. I., and Flindt, M. R. (2018). Agent based modelling (ABM) of eelgrass (*Zostera marina*) seedbank dynamics in a shallow Danish estuary. *Ecological Modelling* **371**, 60–75. doi:10.1016/J.ECOLMO DEL.2018.01.001
- Lillebø, A. I., Neto, J. M., Flindt, M., Marques, J., and Pardal, M. (2004). Phosphorous dynamics in a temperate intertidal estuary. *Estuarine, Coastal and Shelf Science* **61**(1), 101–109. doi:10.1016/J.ECSS.2004.04.007
- Matheson, F. E., Reed, J., Dos Santos, V. M., Mackay, G., and Cummings, V. J. (2017). Seagrass rehabilitation: successful transplants and evaluation of methods at different spatial scales. *New Zealand Journal of Marine and Freshwater Research* **51**(1), 96–109. doi:10.1080/00288330.2016.1265993
- Maxwell, P. S., Eklöf, J. S., van Katwijk, M. M., O'Brien, K. R., de la Torre-Castro, M., Boström, C., Bouma, T. J., Krause-Jensen, D., Unsworth, R. K. F., van Tussenbroek, B. I., and van der Heide, T. (2017). The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems – a review. *Biological Reviews of the Cambridge Philosophical Society* **92**(3), 1521–1538. doi:10.1111/BRV.12294
- McLennan, M., and Sumpton, W. (2005). The distribution of seagrasses and the viability of seagrass transplanting in the Broadwater, Gold Coast, Queensland. *Proceedings of the Royal Society of Queensland* **112**, 31–38.
- McLeod, E., Chmura, G., Bouillon, S., Salm, R., Björk, M., Duarte, C., Lovelock, C., Schlesinger, W., and Silliman, B. R. (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment* **9**, 552–560. doi:10.1890/110004
- Mirfenderesk, H., and Tomlinson, R. (2008). Observation and analysis of hydrodynamic parameters in tidal inlets in a predominantly semidiurnal regime. *Journal of Coastal Research* **24**(5), 1229–1239. doi:10.2112/06-0649.1
- Moksnes, P.-O., Gullström, M., Tryman, K., and Baden, S. (2008). Trophic cascades in a temperate seagrass community. *Oikos* **117**(5), 763–777. doi:10.1111/J.0030-1299.2008.16521.X
- Morton, R. M. (1992). Fish assemblages in residential canal developments near the mouth of a subtropical Queensland estuary. *Marine and Freshwater Research* **43**(6), 1359–1371. doi:10.1071/MF9921359
- Natura Pacific (2012). An underwater treasure: seagrass health and abundance on the Gold Coast. Available at <https://www.natura-pacific.com/an-underwater-treasure-seagrass-health-and-abundance-on-the-gold-coast/> [Verified 30 October 2019].
- Nelson, W. G. (2017). Development of an epiphyte indicator of nutrient enrichment: threshold values for seagrass epiphyte load. *Ecological Indicators* **74**, 343–356. doi:10.1016/J.ECOLIND.2016.11.035
- Nordlund, L. M., Jackson, E. L., Nakaoka, M., Samper-Villarreal, J., Becar-Carretero, P., and Creed, J. C. (2018). Seagrass ecosystem services – what's next? *Marine Pollution Bulletin* **134**, 145–151. doi:10.1016/J.MARPOLBUL.2017.09.014
- Orth, R. J., Harwell, M. C., and Inglis, G. J. (2006). Ecology of seagrass seeds and seagrass dispersal processes. In 'Seagrasses: Biology, Ecology and Conservation'. (Eds A. W. D. Larkum, R. J. Orth, and C. M. Duarte.) pp. 111–133. (Springer: Dordrecht, Netherlands.)
- Orth, R. J., Moore, K. A., Marion, S. R., Wilcox, D. J., and Parrish, D. B. (2012). Seed addition facilitates eelgrass recovery in a coastal bay system. *Marine Ecology Progress Series* **448**, 177–195. doi:10.3354/MEPS09522
- Rasheed, M. A. (2004). Recovery and succession in a multi-species tropical seagrass meadow following experimental disturbance: the role of sexual and asexual reproduction. *Journal of Experimental Marine Biology and Ecology* **310**(1), 13–45. doi:10.1016/J.JEMBE.2004.03.022
- Seagrass-Watch (2015). Gold Coast. Available at <http://www.seagrass-watch.org/GoldCoast.html> [Verified 5 June 2015].
- Short, F., Carruthers, T., Dennison, W., and Waycott, M. (2007). Global seagrass distribution and diversity: a bioregional model. *Journal of Experimental Marine Biology and Ecology* **350**(1–2), 3–20. doi:10.1016/J.JEMBE.2007.06.012
- Short, F. T., Williams, S. L., Carruthers, T. J. R., Waycott, M., Kendrick, G. A., Fourqurean, J. W., Callabine, A., Kenworthy, W. J., and Dennison, W. C. (2010). *Zostera muelleri*: species code: Zc. In 'The IUCN Red List of Threatened Species', 2010. e.T173384A7004901. (International Union for Conservation of Nature and Natural Resources.) Available at <https://www.iucnredlist.org/species/173384/7004901> [Verified 28 February 2011].
- Sievers, M., Brown, C. J., Tulloch, V. J. D., Pearson, R. M., Haig, J. A., Turschwell, M. P., and Connolly, R. M. (2019). The role of vegetated coastal wetlands for marine megafauna conservation. *Trends in Ecology & Evolution* **34**(9), 807–817. doi:10.1016/J.TREE.2019.04.004
- Smith, T., York, P., Macreadie, P., Keough, M., Ross, D., and Sherman, C. (2016). Spatial variation in reproductive effort of a southern Australian seagrass. *Marine Environmental Research* **120**, 214–224. doi:10.1016/J.MARENRES.2016.08.010
- Suchanek, T. H. (1983). Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidea) bioturbation. *Journal of Marine Research* **41**, 281–298. doi:10.1357/002224083788520216
- Unsworth, R. K. F., McKenzie, L. J., Collier, C. J., Cullen-Unsworth, L. C., Duarte, C. M., Eklöf, J. S., Jarvis, J. C., Jones, B. L., and Nordlund, L. M. (2019). Global challenges for seagrass conservation. *Ambio* **48**(8), 801–815. doi:10.1007/S13280-018-1115-Y
- Valdemarsen, T., Canal-Vergés, P., Kristensen, E., Holmer, M., Kristiansen, M. D., and Flindt, M. R. (2010). Vulnerability of *Zostera marina* seedlings to physical stress. *Marine Ecology* **418**, 119–130. doi:10.3354/MEPS08828
- Valdemarsen, T., Wendelboe, K., Egelund, J., Kristensen, E., and Flindt, M. (2011). Burial of seeds and seedlings by the lugworm *Arenicola marina* hampers seagrass (*Zostera marina*) recovery. *Journal of Experimental Marine Biology and Ecology* **410**, 45–52. doi:10.1016/J.JEMBE.2011.10.006
- Valentine, J., Duffy, J. W. D., Larkum, A., Orth, R., and Duarte, C. (2006). The central role of grazing in seagrass ecology. In 'Seagrasses: Biology, Ecology and Conservation'. (Eds A. W. D. Larkum, R. J. Orth, and C. M. Duarte.) pp. 463–501. (Springer: Dordrecht, Netherlands.)
- van der Heide, J., van Nes, E. H., Geerling, G. W., Smolders, A. P. J., and Bouma, T. J. (2007). Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. *Ecosystems* **10**(8), 1311–1322. doi:10.1007/S10021-007-9099-7
- van Katwijk, M., Thorhaug, A., Marba, N., Orth, R., Duarte, C., Kendrick, G., Althuizen, H. J. I., Balestri, E., Bernard, G., Cambridge, M., Cunha, A., Durance, C., Giesen, W., Han, Q., Hosokawa, S., Kiswara, W., Komatsu, T., Lardicci, C., Lee, K.-S., and Verduin, J. (2016). Global analysis of seagrass restoration: the importance of large-scale planting. *Journal of Applied Ecology* **53**(2), 567–578. doi:10.1111/1365-2664.12562
- van Wesenbeeck, B., van de Koppel, J., Herman, P. P., Bakker, J., and Bouma, T. (2007). Biomechanical warfare in ecology; negative interactions between species by habitat modification. *Oikos* **116**, 742–750. doi:10.1111/J.0030-1299.2007.15485.X
- Walker, D. I., and McComb, A. J. (1992). Seagrass degradation in Australian coastal waters. *Marine Pollution Bulletin* **25**(5–8), 191–195. doi:10.1016/0025-326X(92)90224-T

- Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Short, F. T., and Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* **106**(30), 12377–12381. doi:[10.1073/PNAS.0905620106](https://doi.org/10.1073/PNAS.0905620106)
- York, P. H., and Smith, T. M. (2013). Research, monitoring and management of seagrass ecosystems adjacent to port developments in central Queensland: literature review and gap analysis. Report CA120018 for the Port Curtis and Port Alma Ecosystem Research & Monitoring Program, Deakin University, Geelong, Vic., Australia.
- York, P. H., Gruber, R. K., Hill, R., Ralph, P. J., Booth, D. J., and Macreadie, P. I. (2013). Physiological and morphological responses of the temperate seagrass *Zostera muelleri* to multiple stressors: investigating the interactive effects of light and temperature. *PLoS One* **8**(10), e76377. doi:[10.1371/JOURNAL.PONE.0076377](https://doi.org/10.1371/JOURNAL.PONE.0076377)

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