

# Effects of local anthropogenic stressors on a habitat cascade in an estuarine seagrass system

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**Abstract.** Recent research has shown that co-occurring primary and secondary habitat-forming species typically support higher biodiversity than do monocultures of the primary habitat-former alone. However, these ‘habitat cascades’ may not be universal and it is important to know whether, when and where positive effects on biodiversity from secondary habitat-forming species change to negative effects. Here, we tested how anthropogenic stressors (fertilisation and sedimentation) and unattached secondary habitat-forming *Ulva* seaweeds affected the primary habitat-forming seagrass, *Zostera muelleri*, and its associated invertebrates in the Avon–Heathcote Estuary, New Zealand. We experimentally stressed *Zostera* by adding different fertilisation and sediment levels. Fertilisation had little impact, whereas even low sedimentation levels had strong negative effects on *Zostera* and its associated fauna. In a second experiment, sediments and *Ulva* were added to seagrass beds and unvegetated mudflats to test whether sediment stress modifies habitat cascades. We found again strong negative effects of sediments on *Zostera*, irrespective of spatio-temporal conditions, and that negative effects of sediments on invertebrates were enhanced in the presence of the secondary habitat former. These results highlighted that anthropogenic stressors can destabilise habitat cascades; processes that may be of particular importance in estuaries that are characterised by low biodiversity and stressful environmental conditions.

**Additional keywords:** biodiversity, drifting seaweeds, fertilisation, foundation species, morphology, sedimentation.

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## Introduction

Accumulating evidence suggests that co-occurring primary and secondary habitat-forming species (here also referred to as ‘1st HF’ and ‘2nd HF’ respectively) typically support higher biodiversity than did monocultures of the primary habitat-forming species alone (Altieri *et al.* 2007; Thomsen *et al.* 2010; Bishop *et al.* 2012). However, these ‘habitat cascades’ may not be universal and, from scientific and conservation perspectives, it is important to know whether, when and where positive effects on biodiversity change to negative effects. For example, habitat cascades could break down if secondary habitat formers out-compete primary habitat formers or if environmental stressors negatively affect the primary or secondary habitat formers. Despite the growing literature documenting a positive net effect of secondary habitat-forming species on biodiversity (Altieri *et al.* 2007; Thomsen *et al.* 2010, 2018; Angelini *et al.* 2011), we are not aware of studies that have experimentally tested whether or how stressors may destabilise habitat cascades.

Habitat cascades are common in seagrass beds as epiphytes attach to (Hall and Bell 1988a; Bologna and Heck 1999; Gartner *et al.* 2013), drift algae entangle around (Holmquist 1997; Thomsen 2010; Thomsen *et al.* 2013) and molluscs embed among (Valentine and Heck 1993; Thomsen *et al.* 2013) seagrass leaves.

Seagrasses not only provide habitat for secondary habitat-forming species, but they also stabilise sediments, attenuate waves and sequester carbon (Currás *et al.* 1994; Connolly 1997) and, importantly, increase the abundance and diversity of seagrass-associated fauna (Kohn 1967; Abele 1974; Heck and Orth 1980; Stoner and Lewis 1985; Hall and Bell 1988b; Heck *et al.* 1995; Boström and Bonsdorff 1997; Tuya *et al.* 2014).

All of these ecosystem functions are susceptible to anthropogenic stressors, as evidenced by the decline in seagrass beds around the world (Orth *et al.* 2006; Waycott *et al.* 2009; Short *et al.* 2011). Key human activities that threaten seagrasses include global stressors such as climate change (Diaz-Almela *et al.* 2007; Ehlers *et al.* 2008) and invasive species (Williams 2007), as well as local stressors such as nutrient pollution and increased sediment loads (Erfteemeijer and Lewis 2006; Orth *et al.* 2006; Leoni *et al.* 2008; Waycott *et al.* 2009; Barbier *et al.* 2011; Short *et al.* 2011). These stressors typically co-occur (Burkholder *et al.* 1992; Crain *et al.* 2008; Halpern *et al.* 2008; Ceccherelli *et al.* 2018) and it is, therefore, important to understand direct, indirect and interactive effects on the seagrass themselves and on the associated invertebrates (McGlathery 2001; Thrush *et al.* 2004; Wernberg *et al.* 2012). It is reasonably well studied how fertilisation or sedimentation in isolation affect

seagrasses (Burkepile and Hay 2006; Cabaço et al. 2008; Tuya et al. 2013b, 2015), but it is less known how these stressors interact, whether interactions are dose-dependent and how dose-dependency may affect seagrass-associated invertebrates. Furthermore, excessive amounts of nutrients typically stimulate growth of seaweeds inhabiting seagrass beds, thereby favouring epiphytes and drift seaweeds over the seagrasses themselves (Sand-Jensen and Borum 1991; Pedersen and Borum 1996). Nutrient-fuelled growth of epiphytes and drift seaweeds can shade seagrass and cause benthic anoxia (due to respiration and decomposition) below the canopy, and, thereby, stress seagrasses (Cambridge and McComb 1984; Holmer and Bondgaard 2001; Thomsen et al. 2012a). Thus, it is possible that epiphytes and drift seaweeds can both increase and decrease habitat quality for seagrass-associated invertebrates, depending on other environmental stressors, such as nutrient and sediment levels. However, we are not aware of any studies that have tested how the ecological importance of seaweeds within seagrass beds may change from positive or neutral to negative, depending on the environmental context.

We addressed these research gaps by testing whether seagrass performance (here, shoot density and biomass; Roca et al. 2016; Ceccherelli et al. 2018) and associated invertebrate communities (richness, abundance and structure) are negatively affected by (1) sediments and nutrients, and whether these effects are interactive and dose-dependent, and (2) seaweed, and whether these effects are interactive and stronger during the warm season when plant metabolism is higher and invertebrates and seaweed are more abundant. These hypotheses were tested with two experiments in the Avon–Heathcote Estuary, Christchurch, New Zealand. In this system, the primary habitat-forming species is the seagrass *Zostera muelleri*, which is the only seagrass species in New Zealand (Short et al. 2007). *Zostera* is common on sandy substrates and in estuaries throughout New Zealand and temperate Australia (Den Hartog 1970), where it modifies sediment deposition, stabilises substrate and provides habitat for drift seaweed and invertebrates (Ferrell and Bell 1991; Connolly 1994a, 1994b; Fonseca et al. 2011). The secondary habitat-forming seaweed species were sheet-forming *Ulva* spp. (dominated by *U. curvata*), that can form dense mats in estuaries in New Zealand (Jones et al. 2005; Marsden and Bressington 2009; Marsden and Maclaren 2010) and worldwide (Fletcher 1996).

## Materials and methods

Study sites were located in the Avon–Heathcote Estuary (AHE, 43°33'11.7"S, 172°44'39.4"E), where *Zostera muelleri* and *Ulva* spp. are common (hereafter, referred to by their genus names; Jones et al. 2005; Thomsen et al. 2016). The AHE is bordered by Christchurch (population size of ~400 000) and freshwater enters from the Avon (north) and Heathcote (south-west) rivers (McClatchie et al. 1982). Compared to other estuaries in New Zealand, the AHE is relatively eutrophied (Webb 1972) because the tributaries receive large amounts of nutrients (Heathcote and Avon; Boffa Miskell Limited 2015) and sediments (Findlay and Kirk 1988) from intensive agriculture and livestock farming on the surrounding Canterbury plains. The estuary is ~8 km<sup>2</sup> and is predominantly intertidal, with a tidal range between 2.2 m at spring tides and 1.7 m at neap tides (Findlay and Kirk 1988). During high tide, the maximum depth is 5.5 m in the deepest

channel (Webb 1972), whereas during low tide, 85% of the estuary is characterised by intertidal mudflat (Hollever and Bolton-Ritchie 2016). The study area was located in the eastern part of the estuary, close to the Brighton Spit, between 'Tern' and 'Plover' streets.

### Experiment 1: testing for interactive effects of eutrophication and sedimentation on seagrass and associated invertebrates

The first experiment tested the hypothesis that there are interactive effects of sediment and nutrient stress on seagrass performance and seagrass-associated invertebrates. More specifically, we tested for interactive effects between four sediment and four fertilisation levels on *Zostera* biomass and shoot density, and on invertebrate community structure.

We established 25 × 25-cm plots, separated by a minimum of 2 m, in an intertidal seagrass bed. Prior to experimental manipulations, shoot density was counted in each plot centre within a 10 × 10-cm quadrat. Sedimentation was manipulated by adding 0 (control), 1, 2 or 4 cm of sediments, corresponding to sediment levels added in many other seagrass–sediment stress experiments (Cabaço and Santos 2007). Sediments were collected from an adjacent mudflat and sieved using a 1-cm sieve to remove macroinvertebrates, shells, stones and seaweeds. Sediments were added to plots by slowly drizzling the unconsolidated sieved sediment over each plot until the required depth was reached (as in Airoidi and Virgilio 1998). Fertilisation was manipulated by inserting 0, 2, 4 or 8 Jobs Fertilizer Spikes (13% N, 4% phosphate and 5% potash, corresponding to 0.16 g N, 0.05 g P and 0.06 g K per spike) into the sediments within the plots, in a crossed design. Each treatment combination was replicated three times and the total experimental area covered ~48 m<sup>2</sup> (clonal integration was maintained; Tuya et al. 2014). These nutrient concentrations and methods are common for fertilisation experiments in seagrass beds (Worm et al. 2000; Burkepile and Hay 2006). The experiment was conducted over 4 weeks in February–March (summer) 2016. Sediment levels were maintained every 5 days by adding new sediments to plots where sediments had eroded. Fertiliser was re-applied after 2 weeks, corresponding to a total addition of 2.56 g N m<sup>-2</sup> and 0.79 g P m<sup>-2</sup> for the lowest and 10.23 g N m<sup>-2</sup> and 3.15 g P m<sup>-2</sup> for the highest application level. Three days before the experiment ended, a 5-cm silver stick was inserted 4 cm into the sediment (1.2-mm diameter, 99% Ag) in the centre of each plot to measure the depth of the sulfide layer in the sediment, as a proxy for oxygen penetration (as in Holmer et al. 2009, 2011; Thomsen et al. 2012a). At the end of the experiment, silver sticks were first collected, whereafter 64-cm<sup>2</sup> circular cores, pushed 10 cm into the sediment, were collected from each plot centre. Each core was washed in the field in a 1-mm mesh bag to retain seagrass, seaweed and fauna, before being transported to the laboratory for processing.

### Experiment 2: testing sedimentation effects on the habitat cascade

The second experiment tested whether sedimentation destabilises seagrass–seaweed habitat cascades. More specifically, we tested whether addition of sediments affects invertebrate communities, and whether these effects are influenced by seaweeds,

elevation level and seasons. This experiment had the following design: two levels of *Zostera* ( $\pm 1$ st HF; mud v. *Zostera*)  $\times$  2 levels of *Ulva* ( $\pm 2$ nd HF; mud v. *Ulva*)  $\times$  2 sedimentation levels ( $\pm$ addition of sediment)  $\times$  2 elevation levels (intertidal v. shallow subtidal)  $\times$  2 seasons (summer v. winter)  $\times$  3 replicates. Sediments and fronds of *Ulva* were collected from the study site. Sediments were sieved as in the previous experiment and *Ulva* fronds were rinsed and shaken to remove macroinvertebrates. Again, 25  $\times$  25-cm plots separated by a minimum of 2 m were established in both a seagrass bed and on an adjacent mudflat, covering an area of  $\sim 50$  m<sup>2</sup> (clonal integration was maintained; Tuya *et al.* 2014). Shoot density was estimated as in the previous experiment, before 2.8 g WW of *Ulva* was added around the seagrass leaves by pegging them flush into the sediment with two u-bent 20-cm metal pegs. Pegs were also added to the control plots to avoid confounding treatments by the presence of pegs. Finally, 1 cm of sediments was added to the ‘sedimentation’ treatments, using similar methods as in the previous experiment (the lowest level was applied in Experiment 1 that still had an adverse effect on seagrass; see Results section). The experiment ran for 2 weeks in July and the entire experiment was repeated in November 2016. Maintenance was performed every 5 days, adding new sediments and new *Ulva* fronds where necessary. Three days before the experiment was terminated, sulfide oxidation was measured with silver sticks and cores were collected as described in the previous experiment. Note that *Ulva* in this experiment can be considered to be both a primary and secondary habitat former, depending on whether it was collected from the mudflat or from the seagrass bed (Edgar and Robertson 1992; Thomsen *et al.* 2012b, 2013). Finally, we also note that ‘season’ and ‘elevation’ technically are unreplicated test factors (Hurlbert 1984) because we included only one summer, one winter, one subtidal and one intertidal experiment. Our aim here was primarily to test whether effects of *Ulva* are consistent in space and time, and references to ‘seasonal’ and ‘elevational’ effects are, therefore, of less importance (still, we included a cold and a warm month and subtidal and intertidal elevations, to cover a wide range of ambient abiotic conditions, and they were, therefore, treated as fixed factors in statistical analyses).

#### Laboratory analysis

In the laboratory, core samples were rinsed onto a 1-mm sieve to retain macroinvertebrates, seagrasses and seaweeds. Seaweeds and seagrasses (split to above-ground leaves and below-ground roots and rhizomes) were weighed after 48 h of drying at 55°C or until no further weight loss could be detected. All invertebrates were counted and identified to operational taxonomic units (conspicuous taxa to species level, small inconspicuous taxa to orders or families) with a dissecting microscope ( $\times 40$  magnification). Silver sticks were processed by measuring the distance to the blackened part with a digital caliper (blackening is a result of reduction of Ag to Ag<sub>2</sub>S).

#### Statistical analysis

We tested for effects of fertilisation and addition of sediment and macroalgae on (1) distance of blackened silver sticks, (2) seagrass above (leaves) and below (roots and rhizomes) ground biomass, (3) seagrass shoot density, (4) total invertebrate

abundance, (5) invertebrate taxonomic richness and (6) invertebrate multivariate community structure. Invertebrate counts were square-root transformed to reduce the statistical importance of a few highly dominant taxa and to decrease variances for the most abundance taxa. Responses were analysed with permutational-based factorial ANOVA (PERMANOVA+, in the PRIMER software package, PRIMER-e Empowering Research, Massey University, Auckland, New Zealand; Clarke and Warwick 2001). Analyses of the univariate variables were based on Euclidean distances, whereas the Bray–Curtis similarity coefficient was used to test for effects on multivariate community structure. All test factors were considered fixed. Results were considered significant if  $P \leq 0.05$ . We also calculated eta-squared ( $\eta^2 = SS_{\text{test-factor}} \div SS_{\text{total}}$ ) to compare the relative importance of the different test factors. Significant results for test factors with more than two levels were followed by posthoc pairwise Student’s *t*-tests. Finally, the biomass of *Zostera* leaves and *Ulva* was correlated against total invertebrate abundance and richness, using Spearman’s rank correlation coefficient on all samples from the two experiments with and without sediment stress (fertilised samples were classified as ‘unstressed’ because nutrients did not inhibit seagrass or invertebrates; see Results section).

## Results

### Experiment 1: effects of nutrients and sedimentation

#### Silver sticks and seagrass

There was no difference in the depth of the oxidation layer across the treatments (Table 1, Fig. 1a). However, there were significant negative effects of sedimentation (S) on leaf biomass, and root biomass and shoot density ( $P < 0.003$ , Table 1,  $\eta^2 = 87, 37$  and 89% respectively), but no effects of fertilisation. Posthoc pairwise comparisons showed, as expected, highest seagrass shoot densities, leaf biomass and root biomass in control plots ( $S_0 > S_1 > S_2 = S_4$ , Fig. 1b;  $S_0 > S_1 \geq S_4 \geq S_2$ , Fig. 1c;  $S_0 > S_1 = S_2 = S_4$ , Fig. 1d).

#### Invertebrate abundances

We found 350 invertebrates, representing 12 taxa, in the 48 samples. The most important taxa were *Austrovenus stutchburyi* (194 individuals), juvenile crabs (33) and the trochids *Diloma subrostrata* (24) and *Micrelenchnus tenebrosus* (19). Invertebrate abundance was significantly affected only by sedimentation (Table 1, Fig. 1e), with highest abundances in the control plots ( $12.50 \pm 1.0$  individuals per 64 cm<sup>2</sup>), intermediate abundances at 1- and 2-cm treatments ( $6.75 \pm 1.1$  and  $5.75 \pm 0.9$ ) and lowest abundances in 4-cm treatments ( $4.17 \pm 0.7$ ;  $S_0 > S_1 = S_2 > S_4$ , Fig. 1e).

#### Invertebrate richness

There was a significant fertilisation  $\times$  sedimentation interaction on invertebrate richness ( $P = 0.001$ ,  $\eta^2 = 33\%$ , Table 1), showing a stronger negative effect of sedimentation at the highest fertilisation level (Fig. 1f). Irrespective of this interaction, sedimentation was highly significant ( $P = 0.001$ ,  $\eta^2 = 39\%$ , Fig. 1f), with more taxa in the control plots ( $4.48 \pm 0.3$  taxa per 64 cm<sup>2</sup>) than in the sediment treatments ( $2.92 \pm 0.3$ ,  $2.75 \pm 0.4$  and  $2.42 \pm 0.3$ ;  $S_0 > S_1 = S_2 = S_4$ , Fig. 1e).

**Table 1. Overview of permutational-based ANOVA results**

All test factors were considered fixed. Values represent the percentages of the sum of squares out of the total sum of squares (i.e.  $\eta^2$ ). See Tables S1 and S2, available as Supplementary material to this paper, for complete PERMANOVA tables. NO TEST refers to habitat conditions with only mud or *Ulva* (primary habitat former, 1st HF) and is, therefore, irrelevant for the *Zostera* responses. Note that *Ulva* in Experiment 2 can be considered to be both a primary habitat former (1st HF) and a secondary habitat former (2nd HF), depending on whether it was collected from the mudflat or from the seagrass bed. Significant values are in bold. \*,  $P = 0.05-0.01$ ; \*\*,  $P = 0.01-0.001$ ; \*\*\*,  $P < 0.001$

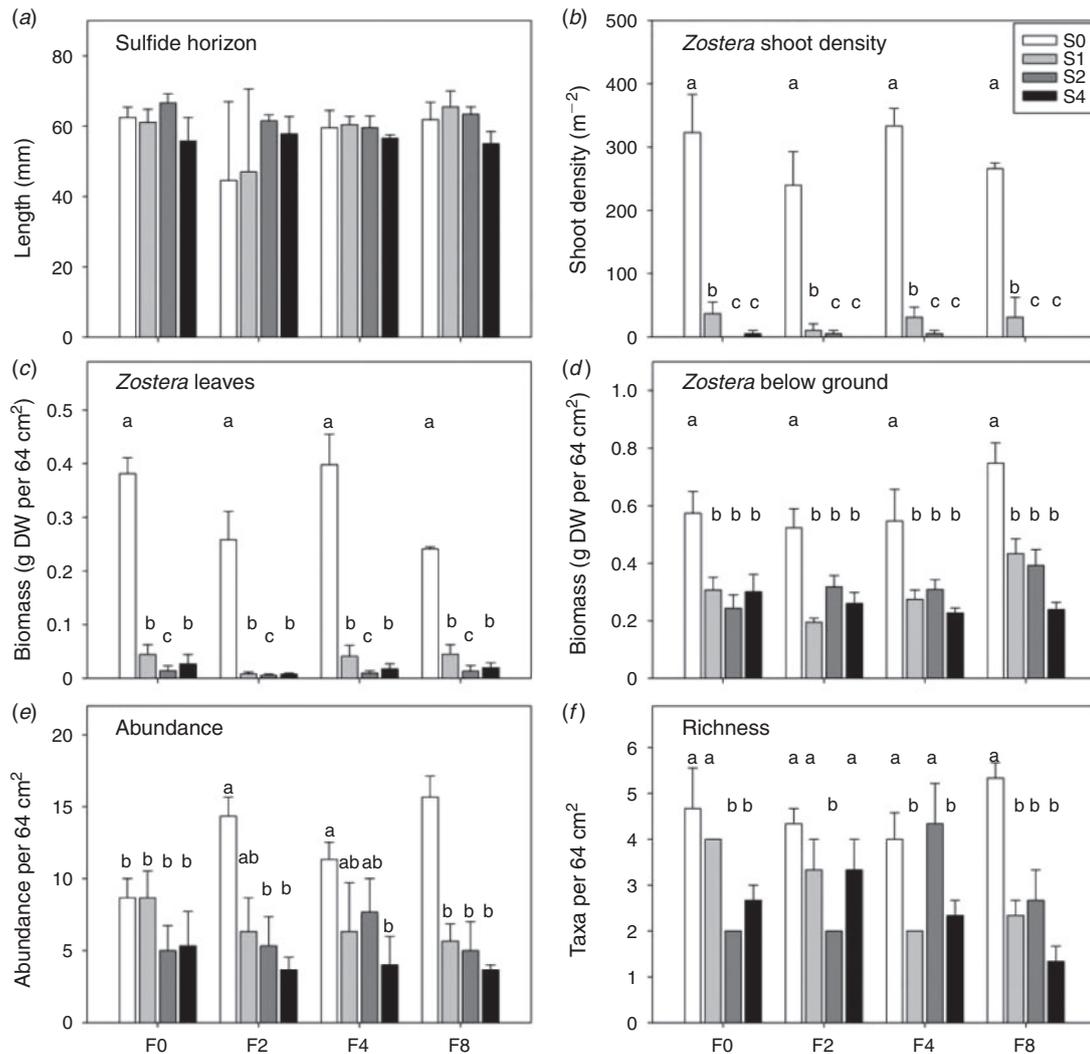
Factor	Silver stick (%)	<i>Zostera</i> Leaves (%)	<i>Zostera</i> below ground (%)	<i>Zostera</i> shoot density (%)	Abundance (%)	Richness (%)	Community Structure (%)
Experiment 1							
Fertilisation (Fer)	6.70	2.28	5.54	0.80	0.04	2.45	4.91
Sedimentation (Sed)	3.43	<b>86.88***</b>	<b>36.79**</b>	<b>89.27***</b>	<b>47.53***</b>	<b>38.68***</b>	<b>14.19**</b>
Fer × Sed	7.68	1.82	5.46	0.94	10.23	<b>32.89***</b>	16.42
Experiment 2							
2nd HF	0.23	1.22	1.72	<b>1.60*</b>	0.73	0.01	<b>4.82***</b>
1st HF	0.24	NO TEST	NO TEST	NO TEST	0.16	0.19	<b>4.52***</b>
Sedimentation (Sed)	3.71	<b>51.19***</b>	0.02	<b>65.11***</b>	<b>36.02***</b>	<b>39.23***</b>	<b>13.24***</b>
Elevation (Ele)	2.09	0.47	2.29	0.08	0.57	0.00	1.48
Season (Sea)	0.20	<b>11.35***</b>	<b>42.57***</b>	0.35	<b>2.75**</b>	1.41	<b>4.72***</b>
2nd HF × 1st HF	1.85	NO TEST	NO TEST	NO TEST	0.04	0.25	0.60
2nd HF × Sed	2.68	1.15	2.00	0.70	<b>1.79*</b>	0.04	1.19
2nd HF × Ele	1.48	0.64	0.20	<b>1.19*</b>	<b>4.48**</b>	<b>2.73*</b>	0.81
2nd HF × Sea	0.87	0.16	0.00	0.05	1.65	0.49	1.23
1st HF × Sed	0.16	NO TEST	NO TEST	NO TEST	<b>6.04***</b>	1.73	<b>2.38**</b>
1st HF × Ele	0.02	NO TEST	NO TEST	NO TEST	<b>6.16***</b>	<b>9.06***</b>	<b>2.31***</b>
1st HF × Sea	2.05	NO TEST	NO TEST	NO TEST	0.90	<b>2.20*</b>	0.94
Sed × Ele	0.08	0.70	0.34	0.35	<b>3.55**</b>	1.35	<b>2.18**</b>
Sed × Sea	1.57	<b>16.16***</b>	0.15	<b>21.11***</b>	<b>2.41*</b>	0.01	<b>2.20**</b>
Ele × Sea	0.76	0.01	1.03	0.43	0.37	1.34	<b>1.95*</b>
2nd HF × 1st HF × Sed	0.56	NO TEST	NO TEST	NO TEST	0.01	0.43	0.33
2nd HF × 1st HF × Ele	4.89	NO TEST	NO TEST	NO TEST	0.00	0.24	0.40
2nd HF × 1st HF × Sea	1.36	NO TEST	NO TEST	NO TEST	0.29	0.31	0.58
2nd HF × Sed × Ele	1.36	0.09	0.10	0.67	0.09	0.46	1.20
2nd HF × Sed × Sea	0.47	0.04	<b>5.60*</b>	0.28	0.36	1.15	<b>2.07**</b>
2nd HF × Ele × Sea	0.03	0.06	0.05	0.03	0.02	0.02	1.25
1st HF × Sed × Ele	0.71	NO TEST	NO TEST	NO TEST	0.36	0.14	0.39
1st HF × Sed × Sea	0.01	NO TEST	NO TEST	NO TEST	0.22	0.02	0.22
1st HF × Ele × Sea	0.05	NO TEST	NO TEST	NO TEST	0.28	1.92	1.19
Sed × Ele × Sea	1.50	1.02	0.07	0.06	0.00	0.00	0.89
2nd HF × 1st HF × Sed × Ele	2.12	NO TEST	NO TEST	NO TEST	<b>1.81*</b>	0.13	0.45
2nd HF × 1st HF × Sed × Sea	0.00	NO TEST	NO TEST	NO TEST	0.00	1.78	0.55
2nd HF × 1st HF × Ele × Sea	1.34	NO TEST	NO TEST	NO TEST	0.01	0.38	0.30
2nd HF × Sed × Ele × Sea	0.06	0.27	0.12	0.26	0.11	0.36	0.77
1st HF × Sed × Ele × Sea	0.00	0.00	0.00	0.00	0.00	0.25	<b>1.78*</b>
2nd HF × 1st HF × Sed × Ele × Sea	0.00	NO TEST	NO TEST	NO TEST	0.11	0.00	<b>1.51*</b>

### Invertebrate community structure

Sedimentation also significantly affected multivariate community structure ( $P = 0.01$ ,  $\eta^2 = 14\%$ , Table 1) but there were no effects of fertilisation or of the sedimentation × fertilisation interaction. The multidimensional scaling (MDS) plot showed a moderate separation between the control plots and the sediment-stressed plots ( $S_0 \neq S_1 = S_2 = S_4$ , Fig. 2). Only two taxa, namely, *Austrovenus stutchburyi* and small juvenile crabs, accounted for 50% of the variability, with their abundance vectors pointing towards the unstressed control plots (Fig. 2).

### Experiment 2: effects of sedimentation and drift algae Silver sticks and seagrass

There was no difference in the depth of the oxidation layer across the treatments (Table 1, Fig. 3a, b). The biomass of seagrass leaves was affected both by the sedimentation × season interaction ( $P = 0.001$ ,  $\eta^2 = 16\%$ ) and the two single test factors (sedimentation:  $P = 0.001$ ,  $\eta^2 = 51\%$ ; season:  $P = 0.001$ ,  $\eta^2 = 11\%$ ). More specifically, there was a strong negative effect of sediments on seagrass leaves, reducing biomass from  $0.21 \pm 0.0$  to  $0.07 \pm 0.0$  g DW per  $64 \text{ cm}^2$  (Fig. 3c, d, although the significant sedimentation × season interaction suggested

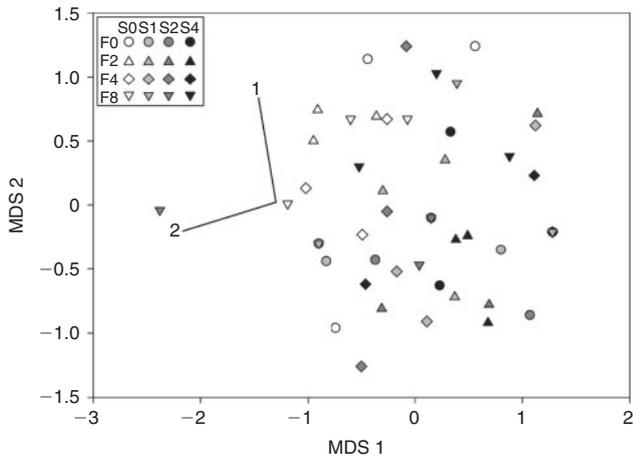


**Fig. 1.** Experiment 1: effects of sedimentation and fertilisation on (a) blackened length of silver sticks, (b) *Zostera muelleri* shoot density, (c) *Z. muelleri* leaf biomass, (d) *Z. muelleri* below-ground biomass, (e) invertebrate abundance and (f) invertebrate richness for four levels of sediment (i.e. addition of 0 ( $S_0$ ), 1 ( $S_1$ ), 2 ( $S_2$ ) and 4 ( $S_4$ ) cm of sediment) and fertiliser (i.e. addition of 0 ( $F_0$ ), 2 ( $F_2$ ), 4 ( $F_4$ ) and 8 ( $F_8$ ) fertiliser sticks). Sample core = 64 cm<sup>2</sup>, error bars = 1 s.e.,  $n = 3$ . Different letters indicate significant differences as detected by permutation-based ANOVA and posthoc pair-wise Student's  $t$ -test comparison (see Table S1, available as Supplementary material to this paper, for corresponding ANOVA analysis).

slightly stronger effects in November than July). For *Zostera* below-ground biomass, we found a complex 2nd HF  $\times$  sedimentation  $\times$  season interaction ( $P < 0.5$ , Table 1,  $\eta^2 = 6\%$ ; Fig. 3e, f) and a more important single-factor seasonal effect ( $P = 0.001$ ,  $\eta^2 = 43\%$ ), showing higher root biomass in November than July ( $0.48 \pm 0.1$  v.  $0.25 \pm 0.0$ ; Fig. 3e, f). Seagrass shoot density was significantly affected by the sedimentation  $\times$  season interaction ( $P = 0.001$ ,  $\eta^2 = 21\%$ ), again with stronger negative effects in November (Fig. 3g). In addition, there was a strong negative single-factor effect of sedimentation ( $P = 0.001$ ,  $\eta^2 = 65\%$ ), reducing densities from  $300.6 \pm 29.8$  to  $63.8 \pm 7.6$  shoots m<sup>-2</sup> (Fig. 3g, h), and a less important, but still significant, effect of the secondary habitat former ( $P < 0.05$ ,  $\eta^2 = 1.6\%$ ), where *Ulva* reduced shoot density from  $197.69 \pm 35.6$  to  $149.86 \pm 28.1$  shoots m<sup>-2</sup> (Fig. 3g, h).

#### Invertebrate abundances

In total, 1036 invertebrates, representing 13 taxa, were counted in the 96 samples. The most abundant were *Austrovenus stutchburyi* (517 individuals), *Micrelenchnus tenebrosus* (222), errant polychaetes (73), *Diloma subrostrata* (73) and the bivalve *Macomona liliana* (41). Statistical results were complex, with seven significant interaction effects (e.g. 1st HF  $\times$  sedimentation, sedimentation  $\times$  elevation, sedimentation  $\times$  season, Table 1). However, most of these effects explained only a small proportion of the total sum of squares of the ANOVA model ( $\eta^2 < 7\%$  for each interaction). Furthermore, compared to others involved in the experiment, these interactions reflected relatively simple interactions, demonstrating that the magnitude of sediment effects was slightly modified by environmental



**Fig. 2.** Experiment 1: effects of sedimentation and fertilisers on invertebrate community structure. The multidimensional scaling (MDS) plot was based on Bray–Curtis similarity for four levels of sediment (different grey scales: i.e. addition of 0 ( $S_0$ ), 1 ( $S_1$ ), 2 ( $S_2$ ) and 4 ( $S_4$ ) cm of sediment) and fertiliser (i.e. addition of 0 ( $F_0$ ), 2 ( $F_2$ ), 4 ( $F_4$ ) and 8 ( $F_8$ ) fertiliser sticks). Data were square-root transformed before analysis ( $n = 3$ , see Table S1, available as Supplementary material to this paper, for corresponding PERMANOVA). A SIMPER analysis was used to determine which species contributed most (up to 50% in the preset study) to the differences found among groups (1: small juvenile crabs, 2: *Austrovenus stutchburyi*). Stress: 0.26.

context (e.g. as in Experiment 1, with a stronger negative effect of sediment in November than in July, Fig. 3i, j). The single most important significant test factor was, as in Experiment 1, a negative effect of sedimentation ( $P = 0.001$ ,  $\eta^2 > 35\%$ , Table 1), which reduced abundances from  $15.38 \pm 1.2$  to  $6.21 \pm 0.5$  individuals per  $64 \text{ cm}^2$  (Fig. 3i, j). Invertebrate abundance, was also affected by season, with higher densities in November ( $12.27 \pm 1.3$ ) than in July ( $9.31 \pm 0.9$ ). Finally, there was a positive net effect of adding *Ulva* to seagrass in July in control plots, but this effect was reversed in treatments with sediments (Fig. 3i, j).

#### Invertebrate richness

There were three significant interaction effects, in concert accounting for 10% of data variability. Sedimentation was again by far the most important significant test factor ( $P < 0.001$ , Table 1,  $\eta^2 = 39\%$ ). Sedimentation decreased the number of taxa from  $4.46 \pm 0.2$  to  $2.40 \pm 0.2$  taxa per  $64 \text{ cm}^2$ , but in contrast to the abundance data, we found no effects of season or adding *Ulva* to *Zostera* beds in either July or November (Fig. 3k, l).

#### Invertebrate community structure

A multivariate analysis of community structure showed eight significant interactions, including a four-factor interaction. However, these interactions accounted for little of the data variability ( $\eta^2 < 3\%$  for each interaction, Table 1). Again, sediment addition alone accounted for most variability ( $\eta^2 > 13\%$ , Table 1) and, as for Experiment 1, the communities in control plots were different from those in the sediment treatments ( $S_0 \neq S_1$ , Fig. 4a, b). Fifty per cent of the multivariate community structure

was explained by six species, but mostly by *M. tenebrosus* and *D. subrostrata*, correlating positively with unstressed control plots in the presence of both *Zostera* and *Ulva* (Fig. 4a, b).

#### Correlations

For the unstressed control plots, invertebrate abundances ( $r_s = 0.36$ ,  $P = 0.005$ , Fig. 5a) and richness ( $r_s = 0.28$ ,  $P = 0.03$ , Fig. 5b) correlated positively with the biomass of *Zostera*, but not *Ulva* ( $P > 0.05$ , Fig. 5c, d). However, no significant correlations were found for sediment-stressed plots ( $P > 0.05$ , Fig. 5a, d).

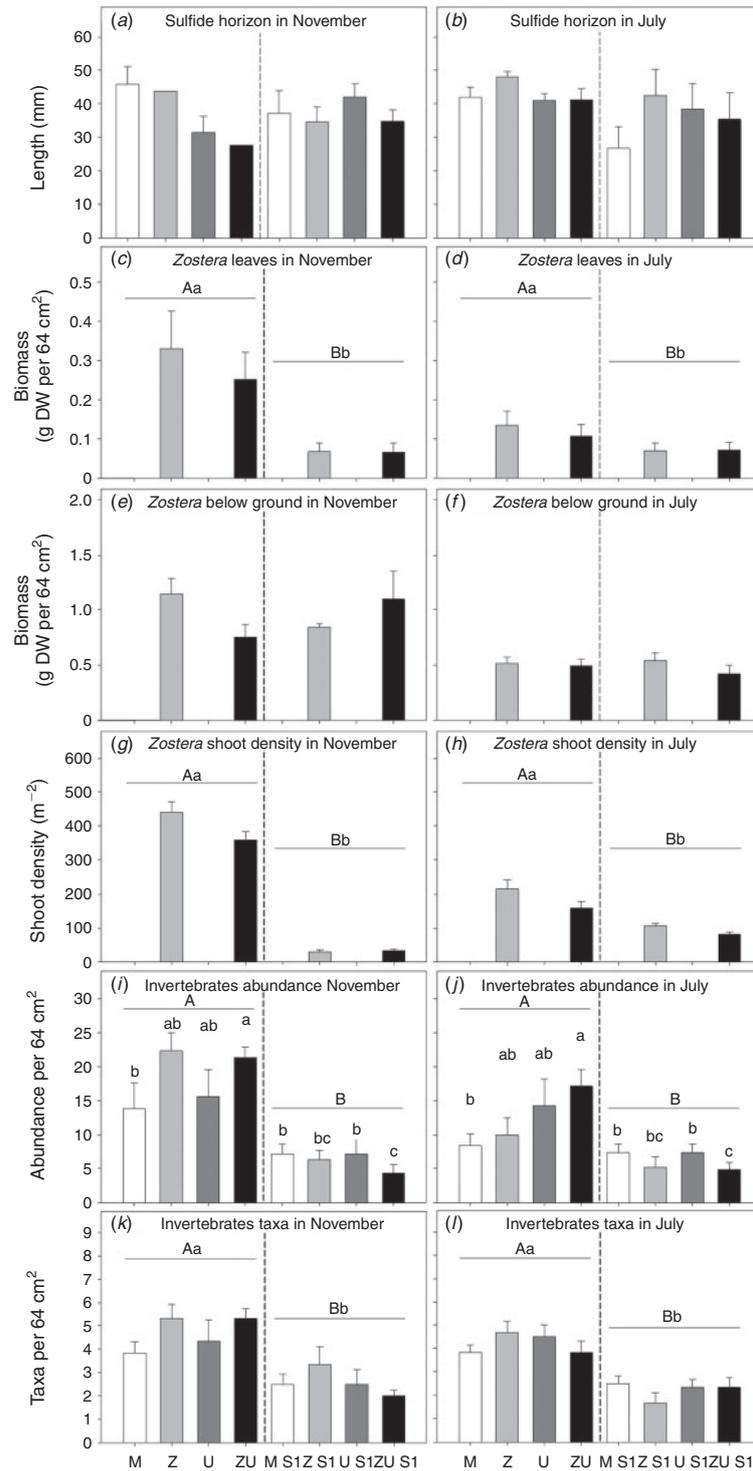
#### Discussion

Here, we have demonstrated strong negative effects of sedimentation on seagrass performance and on seagrass-associated invertebrates. We have also documented a habitat cascade where drifting seaweeds function as secondary habitat formers. This habitat cascade broke down when sediments were added to the seagrass bed, reversing the effects of seaweeds on invertebrates from positive or neutral to negative effects, a pattern that was stronger under warmer conditions. These results provide experimental demonstration of how habitat cascades, which normally enhance biodiversity, can have negative effects on biodiversity under high stress levels.

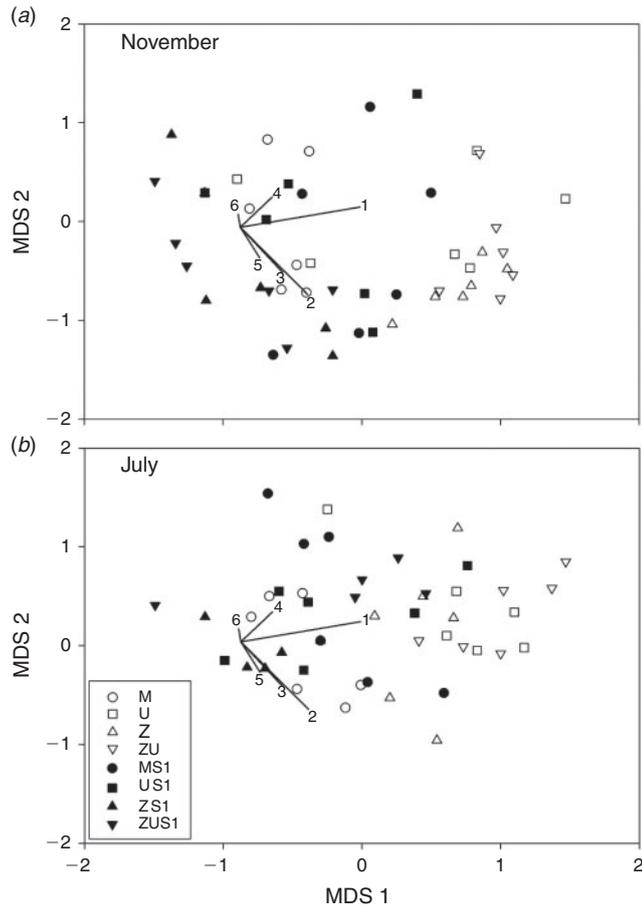
#### Effects on seagrass

Seagrass performance was not affected by synergistic interactions between fertilisation and sedimentation. Synergistic effects have often been assumed to be common when multiple stressors co-occur (Myers 1995; Sala et al. 2000), but empirical evidence has shown that this may not always be the case (Crain et al. 2008; Darling and Côté 2008). Here, the effect of sediment addition overwhelmed any potential much smaller nutrient-addition effects, supporting past experiments that have suggested that estuarine *Zostera muelleri* is insensitive to nutrient concentrations (Morris et al. 2007). However, we did document interactive effects between sedimentation and season, with a stronger negative effect of sediment on seagrasses in the warmer month. It is well established how temperature affects physiological function of seagrasses, such as growth, leaf elongation, photosynthesis, nutrient uptake and respiration (Bulthuis 1987). For example, the congeneric *Z. muelleri* (Kirkman et al. 1982; Larkum et al. 1984; McKenzie 1994; Ramage and Schiel 1999; Turner and Schwarz 2006), *Z. noltii* (Vermaat and Sand-Jensen 1987; Pérez-Lloréns and Niell 1993) and *Z. marina* (McRoy 1970; Sand-Jensen 1975; Jacobs 1979; Nienhuis 1980; Moore et al. 2014) all have higher growth and biomass in summer than in winter. It is likely that the strong inhibition from burial observed in July occurred because *Z. muelleri* had higher growth in this month and, therefore, also potential for more severe inhibition of growth (see references listed above).

There are several possible reasons why we did not find any effects of fertilisation. For example, the applied nutrient levels were low, tidal currents may dissolve the fertilisers and seagrasses from urban estuarine systems may already be long-term adapted (saturated) to high nutrient concentrations. Other fertilisation experiments from less eutrophic estuaries have reported increases in the density, length and biomass of *Zostera* leaves



**Fig. 3.** Experiment 2: effects of adding 1 cm of sediment (S<sub>1</sub>) and drift *Ulva* sp. (U) to muddy (M) and *Zostera muelleri*-dominated (Z) habitats, on (a, b) blackened length of silver sticks, (c, d) *Zostera* leaf biomass, (e, f) *Zostera* below-ground biomass, (g, h) shoot density and invertebrate (i, j) abundance and (k, l) richness in summer (left) and winter (right) seasons. Sample core = 64 cm<sup>2</sup>, error bars = 1 s.e. Data were, for simplicity, pooled across two elevation levels. Different letters indicate significant differences as detected by permutation-based ANOVA and a pair-wise Student's *t*-test comparison ( $n = 6$ , see Table S2, available as Supplementary material to this paper, for the ANOVA table). Capital letters refer to the sedimentation test factor and lower-case letters to the interaction between 1st HF × 2nd HF (HF = habitat former).



**Fig. 4.** Experiment 2: effects of adding 1 cm of sediment ( $S_1$ ) and drift *Ulva* sp. (U) to muddy (M) and *Zostera muelleri* (Z)-dominated habitats, on invertebrate multivariate community structure. The MDS plots were based on Bray–Curtis similarity. To simplicity, the visual interpretation data were split into results from the July and November experiments (but were based on the same analysis, so the two plots can be superimposed on each other) and, therefore, have the same species vectors. Data were square-root transformed before analysis, and, for simplicity, pooled across two elevation levels ( $n=6$ , see Table S2, available as Supplementary material to this paper, for corresponding PERMANOVA). A SIMPER analysis was used to determine which species contributed most (up to 50%) to the differences found among groups (1, *Micrelenchnus tenebrosus*; 2, *Diloma subrostrata*; 3, *Austrovenus stutchburyi*; 4, errant polychaetes; 5, *Macomona liliana*; 6, *Cominella glandiformis*). Stress: 0.26. One outlier sample was removed from the B-plot: ZS<sub>1</sub> (−9.75, 0.00).

when exposed to higher fertilisation levels than in our study (Orth 1977; Morris et al. 2007). Also, leaf nutrient uptake is typically higher than is uptake through roots (Pedersen et al. 1997; Lee and Dunton 1999a, 1999b), especially in nutrient-rich waters (Burkholder et al. 2007; Leoni et al. 2008). In addition, nutrient effects may be stronger in shallow subtidal than intertidal habitats because uptake may be reduced by desiccation stress during low tide. Other studies have also shown that temperature can affect fertiliser dissolution rates (Morris et al. 2007) and seagrass responses to nutrient enrichment (Kaldy 2014). Finally, the low impacts of nutrients may be partly associated with a short experimental duration, as previously

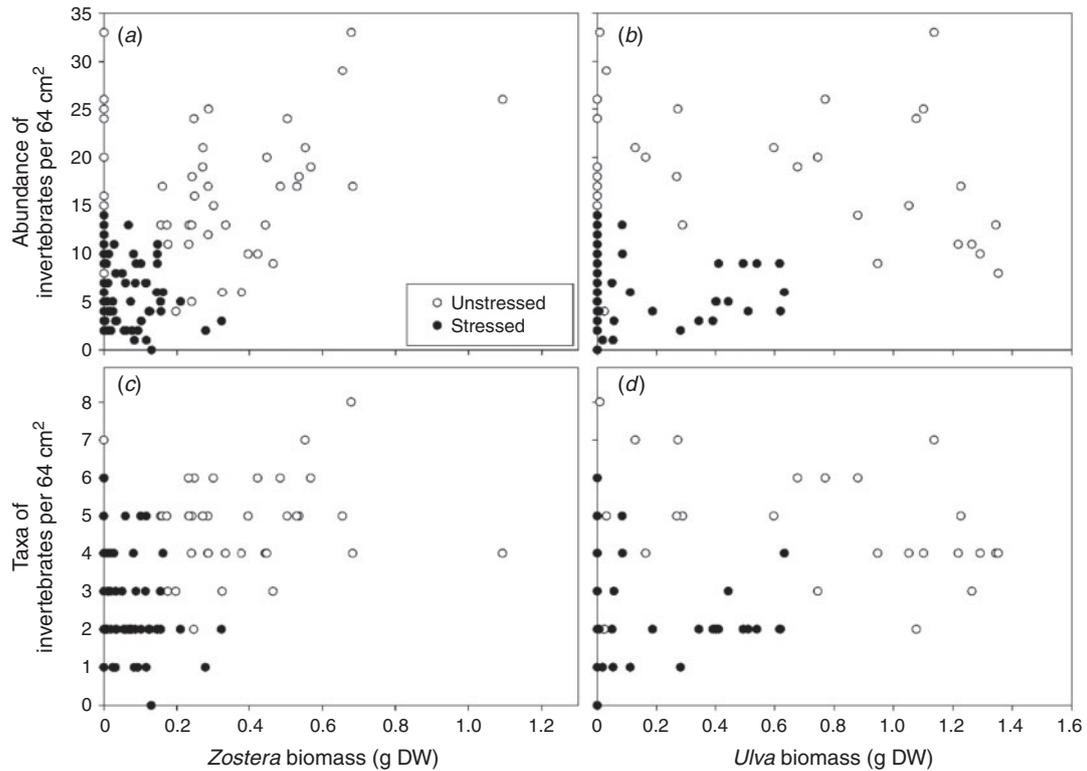
also shown for the seagrass *Cymodocea nodosa* (Ceccherelli and Cinelli 1997).

In contrast to fertilisation, sediment addition dramatically inhibited seagrass biomass even at the lowest application level (1-cm burial). These results are consistent with results from burial experiments with the two congeneric species, *Z. noltii* and *Z. marina*, which experienced 70–90% mortality under 2–4-cm sediment burial (Mills and Fonseca 2003; Cabaço and Santos 2007). However, studies on some seagrass species have shown less negative or even positive effects when buried under low sediment levels, such as observed for *Cymodocea nodosa*, *Posidonia oceanica* and, again, the congeneric species *Z. marina* (Duarte 1995; Manzanera et al. 1998; Mills and Fonseca 2003). As noted by Cabaço and Santos (2007), the different responses may in part be attributed to the size of the seagrass, where smaller species are less likely to survive burial, a ‘size–stress–resistance’ relationship that has also been shown for seaweed–seagrass interactions (Thomsen et al. 2012a). This size effect may be particularly relevant for *Z. noltii* and *Z. muelleri*, because they are smaller than is *Z. marina*.

Addition of the green sheet-forming seaweed *Ulva* also reduced shoot density, as shown in other drift seaweed–seagrass studies (Hauxwell et al. 2001; Brun et al. 2003a, 2003b; Holmer et al. 2011; Thomsen et al. 2012a; Tuya et al. 2013a). The magnitude of *Ulva* effects is likely to be context-dependent, because other studies have shown that effects of drift seaweeds can be more severe at high temperature and high seaweed abundance, and for smaller seagrass species (Thomsen et al. 2012a). It is likely that the negative effect from *Ulva* was caused by light reduction under the seaweeds, limiting growth (Alcoverro et al. 1999; Longstaff and Dennison 1999; Peralta et al. 2002; Brun et al. 2003a) and shoot densities (Longstaff and Dennison 1999; Hauxwell et al. 2001). Another possible inhibition mechanism is that *Ulva* decreases sediment oxygen concentration, although this explanation was not supported by the silver stick data, which suggested that the sediments were well oxygenated irrespective of treatments. Finally, we did not quantify recovery potential of *Z. muelleri*. It is possible that *Z. muelleri* can recover from sediment stress either through encroachment from adjacent clonal plants or by growing up through the sediment, as shown for *Z. noltii* and *Halophila ovalis* (Cabaço et al. 2008), *Halodule uninervis* (Duarte et al. 1997) and *Cymodocea nodosa* (Marbà and Duarte 1995).

#### Effects on invertebrates

Effects of sedimentation on invertebrates varied with fertilisation levels (with stronger negative effects under high fertiliser levels), season and presence of primary and secondary habitat formers (Nichols et al. 1978; Hinchey et al. 2006). Nevertheless, these interactions explained much less of the data variability than did the effect of sediment alone (Table 1; Crain et al. 2008). Survival, growth and stress-escape mechanisms of invertebrates when exposed to sediment stress depend on species-specific adaptations. For example, bivalves are well adapted to burial because of their muscular foot, amphipods can burrow through sediments with their exoskeleton and migrate relatively quickly with their legs (Hinchey et al. 2006), and many deposit-feeding gastropods can move relatively fast under sediments (Bolam 2011). Indeed, many estuarine taxa are resistant to sediment



**Fig. 5.** Correlation between the biomass of (a, c) *Zostera muelleri* and the (b, d) seaweed *Ulva* sp. versus (a, b) abundance and (c, d) taxonomic richness of invertebrates. Experiment 1:  $n = 48$ ; Experiment 2:  $n = 96$ . Black and white points are samples with (stressed) and without (unstressed) sediment addition respectively, and circles and squares represent samples from Experiment 1 and Experiment 2 respectively. Spearman's rank correlation analyses were performed separately for unstressed and stressed samples; stressed:  $r_s = -0.18$ ,  $P = 0.1$  (a),  $r_s = -0.10$ ,  $P = 0.38$  (b),  $r_s = -0.03$ ,  $P = 0.76$  (c), and  $r_s = -0.15$ ,  $P = 0.17$  (d); unstressed:  $r_s = 0.36$ ,  $P = 0.005$  (a),  $r_s = 0.28$ ,  $P = 0.03$  (b),  $r_s = 0.25$ ,  $P = 0.054$  (c), and  $r_s = 0.01$ ,  $P = 0.97$  (d).

burial up to  $\sim 10$ -cm depth (2–5 times higher sediment loading than was applied in the present study) and it is possible that burial depth *per se* is less important than are sediment characteristics such as its grain size or organic matter content (Nichols *et al.* 1978).

Invertebrates were also affected by the biogenic habitat formers *Zostera* and *Ulva*, with particularly strong effect on the molluscs *Micrelenchus tenebrosus*, *Diloma subrostrata* and *Austrovenus stutchburyi*. As previously documented, *Micrelenchus* was abundant on seaweeds (alone, or in combination with *Zostera*; Murphy 2006), *Diloma* on *Zostera* and *Zostera–Ulva* habitats (Hayward *et al.* 2001) and *Austrovenus* in mud and *Zostera* habitats (Morley *et al.* 1997; Hayward *et al.* 1999, 2001; Murphy 2006). There were also strong seasonal effects, with more invertebrates in November than in July. It has previously been shown that seasonal changes in *Z. marina* density affect invertebrates (Laugier *et al.* 1999; Meling-López and Ibarra-Obando 1999; Guidetti *et al.* 2002; Lee *et al.* 2006), because many invertebrates can respond rapidly to changes in habitat availability, habitat complexity (Webster *et al.* 1998; Frost *et al.* 1999; Boström and Bonsdorff 2000) and food availability (Edgar and Robertson 1992; Toyohara *et al.* 1999; Nakaoka *et al.* 2001; Saunders *et al.* 2003). For example, Rueda and Salas (2008) showed a peak in the abundance of epifauna in summer

compared with winter in *Z. marina* habitats, following increases in seagrass leaf size. Above interpretation was supported by significant positive relationships between the biomass of *Zostera* (without sediment stress) and the abundance and richness of invertebrates, as previously documented for *Z. muelleri* (Battley *et al.* 2011) and *Z. marina* (Heck and Wetstone 1977; Mattila *et al.* 1999; Attrill *et al.* 2000). These correlations, again, highlighted that seagrasses increase habitat complexity, buffer environmental stressors (such as desiccation) and provide food for grazers. However, in contrast to other studies with *Ulva* (Thomsen *et al.* 2016) and other seaweeds (Gore *et al.* 1981; Drouin *et al.* 2011), there was no correlation here between *Ulva* biomass and invertebrate data, possibly because high biomass of *Ulva* can smother some invertebrate species (Cardoso *et al.* 2004; Cummins *et al.* 2004).

More invertebrates were found when *Zostera* and *Ulva* co-occurred, than was the case in seagrass monocultures, thereby documenting a habitat cascade (Thomsen *et al.* 2010). Similar habitat cascades have been found in seagrass beds around the world, including Australia (Edgar and Robertson 1992), Denmark (Thomsen *et al.* 2010), Portugal (Cardoso *et al.* 2004), Venezuela (Stoner and Lewis 1985) and Canada (Schneider and Mann 1991), suggesting that this type of habitat cascades may be common. Positive effects of seaweeds were strongest on

gastropods and juvenile crustaceans (cf. the MDS plots), where gastropods probably benefit from the high palatability of *Ulva* (Underwood 1980; Mowles et al. 2011), whereas juvenile crustaceans may benefit more from reduced predation within the *Ulva* mats (Wilson et al. 1990). Importantly, under sediment stress, the effects of *Ulva* (within the seagrass bed) switched from positive or neutral to negative. Under these conditions, seagrass-associated gastropods, that were facilitated by *Ulva* in unstressed control samples, were now greatly reduced, probably because their movement was impaired and their grazing activity reduced (Airoidi and Hawkins 2007). By contrast, other more sediment-tolerant species, including several polychaetes and bivalves, were less affected.

In conclusion, the present study has demonstrated negative effects of sediments on *Z. muelleri* and its associated fauna, and that sediment stress changes effects of seaweeds (within the seagrass bed) on invertebrates, from positive or neutral to negative. A key implication is that if sedimentation increases, for example, if sediment-binding adjacent marshes and mangroves degrade, seagrass and their associated biodiversity could be severely affected.

### Conflicts of interest

The authors declare that they have no conflicts of interest.

### Declaration of funding

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