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Rapid invertebrate responses to macroalgal wrack: two novel field experiments on intertidal mudflats in southern Australia

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Abstract

Macroalgal wrack deposition along coasts is highly variable but it plays an important role in the structure and function of marine communities. To date, most research has focused on the effects of decomposing wrack as it assimilates into the system but little is known about the immediate effects of wrack when it is first deposited in the habitat. Wrack freshly deposited could wash away after a short period (1-2 days) or remain in the habitat and decay depending on tide and weather conditions. To understand the effects of this dynamic resource we experimentally manipulated wrack deposits on intertidal mudflats in Port Phillip Bay, Victoria, Australia. We conducted two experiments using defaunated patches of wrack (300g wet weight) that were a mixture of seagrass and macroalgae and measured community

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responses after two days. The first experiment included real and artificial wrack patches to differentiate between taxa that responded to the biological and physical structure of the wrack. The second experiment using multiple wrack patches to investigate responses to a focal wrack patch that was surrounded by varying number of wrack patches (0, 2 or 4 x 300g wet weight of wrack). Overall, wrack increased abundances and changed invertebrate distributions throughout the wrack and underlying sediment habitat. Mechanisms responsible for immediate taxa responses to the wrack related to the physical structure in the habitat and not biological attributes associated with the real patches. Ostracods and leptostracans were the exception to these patterns with colonization only occurring in wrack and not the artificial wrack. In the multiple patch experiment the majority of the fauna moved vertically into the wrack from the bare sediment and not between surrounding patches of wrack. We suggest specific characteristics, such as invertebrate mobility, feeding mode and sensitivity to changes in sediment condition are important factors that influence individual taxa and overall community responses. Understanding the interactive effects of these characteristics with the characteristics of the wrack (magnitude, frequency, spatial arrangement and composition) is the key to developing predictive models that will inform the management of wrack in marine coastal habitats.

Introduction

Drift algae or macroalgal debris (hereafter termed 'wrack') is an ephemeral 'pulsed resource' that causes periods of increased resource availability in marine environments (Palumbi 2003, Yang et al. 2008). Wrack is typically dislodged during storms or forms from natural die-off and then washes up onto saltmarshes (Minchinton 2002), sandy beaches (Dugan et al. 2003), intertidal rocky shores (Orr et al. 2005) and mudflats (Rossi and Underwood 2002). The production of wrack can be enhanced in areas where nutrient loadings from anthropogenic sources are high (Raffaelli 2000).

Wrack is an essential source of food for benthic invertebrates that feed directly on it or on algae, bacteria or sediment organic matter associated with the wrack (Lopez and Levinton 1987, Franke et al. 2006). It creates habitat in beach surf zones (Baring et al. 2014) and is important mechanism for the dispersal of fish and other marine organisms (Macreadie et al. 2011). If wrack persists in the environment it generally decomposes and assimilates into the sediment, releasing organic carbon and nitrogen (Rossi 2007). This can have indirect effects on primary productivity with consequences for higher trophic levels and food web dynamics (Rossi and Underwood 2002, Dugan et al. 2003, Kelaher and Levinton 2003, Spiller et al. 2010).

However, wrack deposits are highly variable depending on the physical characteristics of the shore, tide, weather conditions, and the type of vegetation in the nearby subtidal habitat (Colombini et al. 2000, Orr et al. 2005, Baring et al. 2014). Different types of macroalgae and seagrass species in the wrack can affect buoyancy characteristics and residency time of the

67 wrack deposits, decomposition and nutritional value or consumption rates by resident taxa
68 (Bishop and Kelaher 2013). Therefore, understanding the effects of wrack is not
69 straightforward (Posey et al. 1995) and will likely depend on a combined understanding of the
70 characteristics of the wrack (magnitude, frequency, spatial arrangement and composition) and
71 characteristics of taxa that respond to the wrack (mobility, feeding mode, tolerance to
72 changes in sediment properties) (Yang et al. 2010). Understanding this relationship is
73 particularly important to inform how, when and if wrack is physically removed, a common
74 management action to improve social and aesthetic values on beaches and coastal habitats
75 that are used recreationally (Mossbauer et al. 2012, Kelly 2014).

76 Recent research has focussed on understanding the variable effects associated with wrack
77 species identity and composition (Moore and Fairweather 2006), the size of the wrack
78 deposit, time since deposition (Olabarria et al. 2007) as well as the combined effects of
79 frequency and magnitude (Bishop and Kelaher 2007). Wrack deposits covering large spatial
80 extents can have wide spread negative effects on benthic fauna before it starts to decompose
81 (Raffaelli 2000) and in the final stages of decomposition as it assimilates into the sediment
82 (Rossi and Underwood 2002, Kelaher and Levinton 2003). Other environmental factors, such
83 as background nutrient loadings, may also play an important role in influencing the variable
84 effects of wrack (O'Brien et al. 2010). Biological response to wrack deposits in areas where
85 background nutrient loadings are high (e.g. close to points of urban-run or river mouth) may
86 be relatively small or negative compared to areas where exposure to anthropogenic sources
87 of nutrients are low (Morris and Keough 2002; Posey et al 2006). In many low energy
88 intertidal habitats the most common form of wrack deposits occur at small magnitudes,
89 creating a mosaic of wrack patches interspaced with bare sediment, which persist only until
90 the next tidal cycle and no greater than two days (O'Brien 2008). The combination of small
91 magnitude, short occurrence and high frequency characteristics of wrack deposits in low
92 energy intertidal habitats has not to our knowledge been investigated, but we expect may be
93 important for predicting the effects of wrack on benthic communities.

94 The aim of this study was to develop an experimental approach that would mimic the natural
95 spatial and temporal scale of wrack deposits on intertidal mudflats and investigate the
96 mechanisms underlying macrofauna community responses. The experimental approach used
97 defaunated wrack patches (300g wet weight) positioned on the mudflats for two days,
98 representing the typical size and frequency of wrack deposits that wash on and off with the
99 tide and wind movement on intertidal mudflats in Port Phillip Bay, Victoria, Australia (O'Brien
100 2008). We conducted two experiments using this approach. The first experiment ('artificial
101 wrack experiment') was repeated over time and space and focused specifically on
102 mechanisms that influence invertebrate consumer responses to wrack. Some taxa are more
103 sensitive to anoxic environments created under large wrack deposits and use the wrack as a
104 refuge (Hull 1987, Raffaelli 2000) while other taxa, commonly mobile herbivores, use it as a
105 source of food (Norkko et al. 2000, Olabarria et al. 2007). To differentiate between these
106 mechanisms we used real and artificial patches of wrack in this experiment and assumed taxa

that utilised the physical structure of the wrack (e.g. as a refuge) would have the same response to the real and artificial patches. Whereas the taxa that responded to food availability or other biological attributes associated with the wrack would show different responses to the real compared to the artificial patches.

The second experiment ('multiple patch experiment') was designed to represent a typical scenario of small-scale wrack deposits, which creates a mosaic of wrack and non-wrack habitats across an intertidal mudflat. The experiment specifically tested the hypothesis that colonisation of wrack by macrofaunal would depend on the number of patches of wrack in the surrounding environment. Based on the rapid responses we detected in the artificial wrack experiment we predicted mobile taxa that typically use wrack as a food source (e.g. ostracods) would be affected by the number of surrounding wrack patches. Whereas, taxa that would not be affected by additional surrounding patches could be sediment-dwelling infauna (e.g. polychaetes) that are found deeper in the sediments (Kelaher and Levinton 2003), are less mobile and influenced only by changes in sediment condition directly under individual wrack patches (Raffaelli 2000).

Methods

Study site

The experiments were conducted on intertidal mudflats in Port Phillip Bay, Victoria, Australia, which are moderately exposed to the prevailing south to southwesterly wind and wave action in the Bay (Figure 1). The mudflats are on the foreshore of Melbourne Water's Western Treatment Plant, which covers 10,851 ha and is one of the main sewage processing plants in Victoria (Steele 1996). The closest sewage outlet is approximately 1 km north of the Beacon Point mudflat and discharges secondarily treated effluent across the intertidal region. Model simulations indicate that the experimental mudflats will be within the influence of the effluent plume but that the effluent will be strongly diluted (between 20-100 fold) by this point (Greer 2012). The sites were mostly unvegetated mud, dominated by corophiid amphipods and the polychaetes, *Capitella* spp. Large numbers of waders and shorebirds (permanent and migratory) forage on the mudflats, which has a mean tidal range of 0.9m and is exposed for 4 to 6 hours during low tide. Pilot data collected prior to these experiments showed wrack deposits on these mudflats were typically comprised of seagrass and macroalgae debris (average wet weight = 300 g m⁻²) that would persist on the mudflats for several tidal cycles or up to two days (O'Brien 2008). Temporal variability in wrack deposition was greatest between weeks, mostly likely reflecting the changes in local weather patterns. Periodic large deposits of wrack caused by storms can persist along the coastline for weeks before decomposing or removal by another storm (Morris and Keough 2003). Examination of the area before the experiments were set-up showed no indication of a recent deposit, such as remains of decomposing algae or areas of anoxia.

Experimental design and sampling

Artificial wrack experiment

This experiment was repeated on two mudflats that were separated by approximately one kilometre - Kirk Point and Beacons Point mudflats (Figure 1). Experimental patches of wrack were all 300 g wet weight and consisted mainly of seagrass (45%) and filamentous brown macroalgae (45%) with some *Ulva* sp. (30%); all common constituents of wrack at these sites (O'Brien 2008). Wrack was collected from the site one week prior to the experiment, rinsed in freshwater to remove fauna and excess sediment. Three randomly chosen defaunated patches were examined under a dissecting microscope to ensure the technique was successful in removing all fauna. The wrack was frozen at -4°C to prevent decomposition before being transported back into the field.

The experiment was conducted in a 50 m x 25 m experimental area located in the mid-littoral zone. To identify general response patterns it was important to repeat the experiment and so we conducted multiple runs of the experiment in consecutive weeks. At Beacons Point, the experiment was repeated in the first and second week of April 2006. At Kirk Point, the experiment was repeated in the first and second week of July 2006 and a third time in March 2007. There were four replicates of each treatment except for the fifth repeat of the experiment at Kirk Point where there were five replicates of each treatment. The experimental treatments were (i) a patch of wrack (W), (ii) a patch of artificial wrack (A), (iii) untouched sediment control (C) and (iv) procedural control (only at Beacons Point). The real and artificial wrack were spread evenly over a 0.16 m^2 area and pinned in the middle of each experimental plot using a 40 x 40 cm plastic gauze mat and six U-shaped pegs to secure the edges. The artificial patch of wrack was 300 g wet weight (same as the real wrack patch) with pieces of cotton that were shredded by hand in different shapes to mimic the different configurations of algae (e.g. *Ulva* sp. leaves versus filamentous algae) and strands of seagrass. The procedural control was only the plastic gauze mat and pegs in the same arrangement as in the treatment plots but minus the real/artificial wrack. This was included in the experiment to identify if the plastic gauze mat and pegs had any influence on fauna responses. Based on the results from Beacons Point, in particular the comparison between the procedural control and untouched control (see results of pairwise comparisons below), the procedural control was not included in the experiment runs at Kirk Point or the multiple patch experiment.

The real and artificial wrack patches were collected 48 hours after set-up to mimic the average time a wrack patch of this size stays on the mudflat. The wrack was collected by carefully placing them in a plastic bag ensuring no fauna escaped and transported back to the laboratory. Once the wrack was removed, one sediment core (100-cm^2 placed 10cm deep) was taken to measure infauna remaining in the sediment underlying the wrack. Two small cores (20 ml syringes with the tip cut-off placed 1cm deep) were taken adjacent to the large core for chlorophyll *a* and sediment organic content analysis. All samples were taken back to

the laboratory in the dark on ice. In the final run of the experiment at Kirk Point, redox potential was measured using a portable TPS Pty Ltd WP-81 meter with a pH combination probe (Ionode Pty Ltd GL20). The probe was inserted through the wrack and placed 1 cm deep into the sediment and once the potential had stabilised the readings were taken. Porewater was sampled directly after the wrack was removed by sampling the sediment to a depth of 5 cm deep with four 20 ml syringes with the top cut off. This sediment was returned to the laboratory for porewater extraction (see below).

Multiple patch experiment

This experiment was conducted in February 2007 on the Kirk Point mudflat (Figure 1). There were 16 plots randomly assigned to one of the following treatments: (i) a patch of wrack (defaunated 'focal patch'), (ii) a patch of wrack (defaunated 'focal patch') surrounded by two additional wrack patches (2W), (iii) a patch of wrack (defaunated 'focal patch') surrounded by four additional wrack patches (4W), (iv) bare sediment control (C). The plots were separated by at least 2 metres and arranged haphazardly in a 50 m x 25 m experimental area on the intertidal mudflat. Wrack was collected from the site for each 'focal patch', defaunated and frozen prior to the experiment (the same approach as used in the artificial wrack experiment). At the start of the experiment, each 'focal patch' was spread evenly over a 0.16 m² area in each plot and pinned in the middle using a plastic gauze mat. The additional surrounding wrack patches for the 2W and 4W treatments were 300 g wet weight and collected from the site on the day the experiment started (i.e. so fauna was still present) and placed 10-20 cm around the 'focal patch' (Supplementary Figure 1). Each 'focal patch' and control plot was sampled 48 hours after the experiment commenced by collecting fauna from the wrack, infauna under wrack, sediment chlorophyll and organic content in the same way as described for the artificial wrack patch experiment. All samples were taken back to the laboratory in the dark on ice.

Laboratory techniques

In the laboratory, the real and artificial wrack patches were rinsed with freshwater, collecting all macrofauna retained on a 500 µm sieve. Infauna from the sediment core was also sieved using a 500 µm mesh. Fauna from the wrack and infauna (from the sediment core) were then preserved in 70 % ethanol before being counted under a dissecting microscope and identified to the lowest possible taxon, which was genus or species for the numerically abundant taxa and family or order for the less common taxa. Sediment samples taken for chlorophyll and organic content analyses were freeze-dried. Chlorophyll was extracted from 0.10 g of sediment with 6 ml of absolute ethanol overnight at 4°C (Jespersen and Christoffersen 1987). The extract was centrifuged at 3500 rpm for 7 minutes and chlorophyll *a* was measured with a spectrophotometer using the equation from Jeffrey and Humphrey (1975). Organic carbon content was determined by loss on ignition (450°C, 4 hours). Sediment from the four syringes was combined and centrifuged (4000 rpm at 4°C) for 10 minutes to extract the porewater

before being filtered through a 0.45µm filter and frozen at -20°C. Samples were analysed for dissolved inorganic nitrogen using a QuikChem 8000 Automated Ion Analyser (Colorado, USA).

Statistical Analyses

Artificial wrack experiment

In all analyses treatment (T) was fixed and run (R) was random and orthogonal to treatment with 4 levels of treatment at Beacons Point (wrack, material, procedural control, control) and 3 levels of treatment at Kirk Point (wrack, material, control). There were 2 levels of run at Beacons Point and 3 levels of runs at Kirk Point. Since the experimental runs at each site were conducted at different times of year we analysed the sites separately and made general comments about the common patterns between sites rather than including site as a factor in the statistical tests. Fauna collected in the wrack and the underlying sediment were combined into one data set ('total fauna'). Infauna were also analysed separately to understand the distribution of individuals between the wrack and underlying sediment ('infauna'). All taxa found in the samples were included in multivariate analyses and only taxa that occurred in >50% samples were used separately in univariate analyses.

Multivariate data were analysed using a factorial PERMANOVA (Anderson 2001) based on Bray-Curtis dissimilarities measures. Data was fourth root transformed prior to analyses. Multiple comparisons between treatment groups for the Beacons Point data were done to determine similarities between the procedural control, control and other treatment groups. When the interaction term was significant ($T \times R$, $P < 0.05$) these multiple comparisons were done for each run separately. Otherwise, multiple comparisons were pooled across experiment run. Non-metric multidimensional scaling (nMDS) ordinations and constrained ordinations using Canonical Analysis of Principal Coordinates (CAP), both based on Bray-Curtis dissimilarity matrices, were used to visualize overall group and interaction differences for the total fauna and infauna communities. Since there were mostly significant interactions between Treatment and Run, the CAP analyses was useful as it allowed us to compare differences between the fauna communities based on the interaction term alone (Anderson and Willis 2003). In most cases the CAP ordinations were good representations of the interactive patterns and discriminated between these *a priori* groupings better than the n-MDS ordinations.

Univariate measures were analysed using 2-factor analysis of variance and planned comparisons. In all analyses, assumptions of normality and homogeneity of variances between groups were checked using box plots and residual plots. When the assumptions were not met and transformation improved this, the analyses were done on transformed data (transformations are reported in figure captions). Otherwise, the analyses were on untransformed data. If the interaction was not significant ($T \times R$, $p > 0.05$) planned comparisons were conducted between treatment groups. The first comparison was between

wrack and material (W v M). If the difference was not significant they were combined and compared to the control (C v M + W). If there was a significant difference between M v W they were compared separately to the control (C v M and C v W). If the overall interaction was significant ($T \times R$, $p < 0.05$) planned comparisons were done in the same way but within each run of the experiment. Porewater nutrients and probe data taken at Kirk Point on run three were analysed using a 1-factor analysis of variance with three levels of Treatment (C, M and W). Planned comparisons between treatments proceeded in the same order as the two factor analyses. Based on our experience conducting experiments at these sites, we predicted that a 50% change would represent a significant biological effect and so calculated the power to detect a 50% change from the control to the material and wrack treatments for all variables that did not have a significant treatment effect.

Multiple patch experiment

Treatment was a fixed factor in all tests with 4 levels (control, 0W, 2W and 4W). Multivariate data were analysed using a factorial PERMANOVA (Anderson 2001) and *a posteriori* multiple comparisons between each level of treatment. Fauna was analysed as total fauna and infauna, as described for the artificial wrack experiment. All analyses were based on Bray-Curtis dissimilarity measures and data were fourth root transformed prior to analyses. If there were insufficient unique permutations, Monte Carlo p-values were reported (Anderson et al. 2008). Multivariate data were graphically represented by non-metric multidimensional scaling (nmMDS) ordinations. One-way analysis of variance tests were used to analyse total number of individuals, total number of taxa and individual macrofauna taxa (taxa that occurred in >50% of samples), sediment organic carbon and chlorophyll *a*. Fauna data were treated the same way as in the multivariate analyses by first analysing the combined wrack and infauna data and then analysing the infauna separately. In all analyses, where the assumptions of normality and homogeneity of variances between groups were not met, data were square root or fourth root transformed. For all analyses with non-significant treatment effects we calculated power to detect a 50% change between the control and 4W treatment, assuming the 4W would have the greatest effect and that the power to detect any changes between control and the other treatments 0W and 2W would be lower.

All multivariate analyses were done using PERMANOVA v1.6 (Anderson 2005) and univariate analyses were done using R 2.4.0 (R Development Core Team 2006). Power was calculated using G*Power 3 (Faul et al. 2007).

Results

Two polychaete taxa, *Capitella* spp. and Nereididae, were found in all samples in both experiments, while polychaetes from the Families Spionidae, Phyllodocidae, Ophellidae, Orbiniidae, Terebellidae, Cirratulidae, and Syllidae were less common and present only

intermittently in the samples. Other taxa that were present in all samples in both experiments were bivalves (*Mysella donaciformis* and *Musculista senhousia*) and the amphipods, *Corophium* sp. and *Gammaropsis* sp.. Ostracoda and Leptostraca were present in both experiments but typically only occurred in the experimental wrack patches and not in controls or sediments underlying the wrack.

Artificial wrack experiment

Beacons Point

There were more than twice as many individuals found at Beacons Point (average 7092 individuals per run) compared to Kirk Point (average 2494 individuals per run).

The composition and abundance of the total fauna communities (wrack and sediment) at Beacons Point depended on both treatment and experimental run (treatment x run <0.05, Table 1). The unconstrained MDS ordination showed no clear groupings between the different runs and treatment groups (ordination not shown).

The constrained CAP ordination on the interaction term was a better representation of these results with significant differences between the treatment combinations ($P = 0.0001$, with 9999 permutations) and clear separations between the controls (C, PC) and treatments (M, W) groups, the main comparisons of interest (Figure 2a).

There was not a significant interaction for the infauna community analyses but significant effects of treatment and run (Table 1). The CAP ordination using the interaction term ($P = 0.0001$, with 9999 permutations) showed clear differences in infauna communities between the two experiment runs but not between treatment groups (Figure 2b).

There were no statistically significant differences between the control and procedural control for the total fauna or infauna community pairwise comparisons (detailed results in Supplementary Table 1). The CAP ordinations support this with similar communities (both total fauna and infauna) associated with the control and procedural control groups (Figure 2a and 2b). To simplify the results sections and focus on our main question of interest, we excluded the PC treatment from the univariate analysis and Kirk Point runs of the experiment as we were confident that community responses were from the actual wrack and material treatments and not from the experimental procedure.

Overall, there tended to be more taxa in the material and wrack treatments (8-15 taxa) compared to the control (7-10 taxa) (Table 2, Figure 3) but there were no differences in total numbers of individuals (Table 2, Figure 3). Some taxa had strong responses to the treatments, such as the leptostracans that occurred only in the wrack treatments and not the material, but this pattern was only evident in the first run of the experiment when leptostracans were most abundant (Figure 3). Ostracods were found in the wrack only and not the material treatment, a pattern that was consistent between runs (Figure 3.).

Other taxa had treatment responses that varied between runs of the experiment. For example, the amphipod *Gammaropsis* sp. had similar numbers of individuals in the material and wrack treatments in the first run of the experiment but fewer numbers of individuals in the wrack compared to the material in the second run (treatment x run < 0.05, Table 2, Figure 3). Most of the other taxa that were analysed individually had responses to the wrack and material treatments that were consistent between runs of the experiments. The bivalves *Musculista senhousia*, *Mysella donaciformis*, amphipod *Corophium* sp., and hydrobiid gastropods were always found in the control plots, underlying sediments as well as in the material and wrack patches (Table 2). Similarly, the polychaete *Capitella* spp. and individuals from the families Spionidae and Nereididae were found mostly in the sediment and not in the material and wrack (Table 2).

When the infauna data was analysed separately there were significantly lower abundances of *Corophium* sp. and *M.senhousia* in the sediment underlying the material and wrack patches compared to the controls (Table 2, Figure 3). Although abundances of these taxa varied between runs of the experiment the patterns of fewer individuals under the material and wrack was consistent (Figure 3). The power to detect an effect size of 50% between the control and treatments (material and wrack) was 45% or more for total number of individuals and all taxa except for Hydrobiidae, which had a power of 6% (Table 2).

There were no effects of treatment on chlorophyll *a* or organic matter but a significant effect of run with more chlorophyll *a* in the first run (mean $\pm$ standard error, $29.7 \pm 1.8\mu\text{g/g}$) compared to the second ($21.2 \pm 1.4\mu\text{g/g}$) and less organic content in the first run ($4.3 \pm 0.2\%$) compared to the second ($5.0 \pm 0.2\%$) (Table 2).

Kirk Point

These results were similar to what we found at Beacons Point with significant interaction between treatment and experiment run (treatment x run < 0.05, Table 1, Figure 2c) and clear differences in the structure and abundances of the total fauna communities (CAP analysis $P = 0.001$, with 9999 permutations). Similarly, the infauna communities were clearly different between the runs of the experiment and some of the treatment groups (CAP analysis $P = 0.001$, with 9999 permutations, Figure 2d)

We found the same wrack-only taxa, as at Beacons Point (ostracods and leptostracans), but only in the third run of the experiment. Therefore, the total number of taxa were greater in the material and wrack treatments compared to the control only in the third run of the experiment (Table 3, Figure 4). There was a 50% decline in total number of individuals across all treatment groups in run 3 compared to the first 2 runs (Figure 4) but no significant effect of treatment on total numbers of individuals in any run of the experiment (Table 3).

We found the same taxa responded to the wrack as in the Beacons Point experiments. Ostracods were most abundant in the wrack compared to the material, particularly in the third run of the experiment when abundances were highest (Table 3, Figure 4). Leptostraca occurred in the material and wrack treatments but only in the third run (Table 3, Figure 4). Abundances of *Gammaropsis* sp. were variable (run 1: 40-50 individuals per plot, run 2: 10-11 individuals, run 3: ~1 individual) but the response to wrack was always the same with individuals occurring in both the material and wrack treatments (Figure 4). At Beacons Point the Nereididae polychaetes were only found in the sediments with no significant difference between the control and treatments but at Kirk Point there was a decline in the material and wrack treatments compared to the control, irrespective of experimental run (Table 3, Figure 4).

There were no effects of treatments on any of the other taxa at Kirk Point (*M.senhousia*, *M.donaciformis*, *Capitella* spp., *Corophium* sp. and Hydrobiidae) but abundances of these taxa were often significantly different between runs of the experiments. *M.senhousia* had a significant interactive effects of treatment and run but when treatment was analysed within each run there were no statistically significant differences (Table 3). The power to detect a 50% change between the treatments and control for all non-significant taxa was high (> 90%) except for Hydrobiidae (6%), *M.donaciformis* (46%) and *Capitella* spp. (48%) (Table 3).

Redox potential and dissolved inorganic nitrogen (DIN) under the material and wrack treatments were similar and statistically significant from the bare sediment controls (Table 3, Figure 4). There were no significant treatment effects on chlorophyll a or organic matter but both were different between runs of the experiment. Overall there was chlorophyll a in the third run of the experiment (mean $\pm$ standard error, 22.0 ± 1.4 μ g/g) compared to the first (14.4 ± 0.6) and second (15.6 ± 0.4) and lower levels of organic content in the second run of the experiment (run 1, $3.2 \pm 0.1\%$; run 2, 2.7 ± 0.1 ; run 3, 4.0 ± 1.4) (Table 3).

Multiple patch experiment

The fauna communities in the wrack plots were significantly different from the fauna communities in the control plots where wrack was not present (Table 4, Figure 5a). The infauna communities under the wrack tended to be different from the infauna communities in the control plots (Figure 5b) although this comparison was not statistically significant. The only significant pairwise comparison for the infauna communities was between the control and 4W wrack treatments (Table 4).

Total numbers of individuals increased in the wrack treatments compared to the control but there were no statistically significant differences between the 0W, 2W and 4W wrack treatments (Table 5, Figure 6). Total number of taxa was also greater in the wrack treatments compared to the control (Table 5, Figure 6). When the infauna data was analysed separately, the pattern was fewer individuals and number of taxa in the sediment under the wrack patches compared to the control (Table 5, Figure 6).

Ostracods and leptostracans were only found in the wrack and not in the control plots or under the wrack. Ostracods increased in abundances with increasing number of surrounding experimental wrack patches (Table 5, Figure 6). Leptostracans were present in very low densities (average of one individual per sample) and only in the wrack patches with no significant differences between wrack treatments (Table 5, Figure 6). *M. donaciformis* (Table 5) was the only other taxa analysed individually that had a significant effect of treatment with higher abundances in the wrack compared to the controls (Table 5, Figure 6). The overall trend was similar for all other taxa (Nereididae, *Capitella* spp., *M. senhousia* and *Corophium* sp.) with higher abundances in the wrack treatments compared to the control but these comparisons were not statistically significant. When infauna was analysed separately, abundances for most taxa were lower under the wrack compared to the control (*M. donaciformis*, *M. senhousia*, *Capitella* spp.; Table 5). Power to detect a 50% effect size between the control and 4W treatment for all non-significant taxa was >50%, except for Orbiniidae and Nereididae in the total fauna calculations (Table 5).

There were no effects of treatment on chlorophyll *a* (mean $\pm$ standard error, 24.4 ± 2.1 $\mu\text{g/g}$) or sediment organic content (3.9 ± 0.2 %) and the power to detect a 50% change in these variables between the treatments and control was high (> 80%) (Table 5).

Discussion

Community responses to the wrack in both experiments were rapid (i.e. within days) and numerically dominated by opportunistic species that were mobile (i.e. not in permanent burrows or attached to the substrate) deposit feeders that feed exclusively on detritus (e.g. *Capitella* spp.) or have flexible feeding modes and can change between suspension feeders and deposit feeding depending on environmental conditions (e.g. *M. senhousia*, *M. doniformis*, *Corophium* sp.) (Hayward and Ryland 1990, Edgar et al. 2005). Most taxa distributed throughout the wrack and underlying sediments (e.g. *M. senhousia*, *M. doniformis*, *Corophium* sp.) while others either remained in the underlying sediment (e.g. Spionidae) or colonized only the wrack patches (leptostracans, ostracods, *Gammaropsis* sp.). Abundances of these taxa were spatially and temporarily variable but the direction of the responses to wrack on the mudflat were generally the same. These findings were consistent with previous studies in other marine habitats, which have documented rapid and numerically abundant invertebrate colonisation of wrack (Norkko and Bonsdorff 1996a, Dugan et al. 2003). Our experiments provide new information about the mechanisms responsible for invertebrate responses to wrack and how the spatial variability of wrack deposits is likely to influence these rapid responses.

Ostracods and leptostracans

At both sites in the artificial wrack experiment there were small increases in the number of taxa in the material and wrack treatments with the presence of wrack-only taxa, such as ostracods, and leptostracans. These mobile, surface-feeding detritivores are often the most abundant taxa in wrack communities (Norkko et al. 2000, Dugan et al. 2003).

We found that ostracods and leptostracans tended to colonise the wrack and not the material but only when abundances were high (e.g. Beacons Point when ~ 17 - 100 individuals per wrack patch). Both these taxa are generalized detritivores that can swim and move across the sediment surface (Armonies 1988) (Armonies 1988) and have been previously shown to feed on algae and particulate organic matter in wrack (Norkko et al. 2000). Although the abundances of these taxa were highly variable between sites and experimental run, when present they colonized the wrack presumably using it as a source of food.

Based on these results, we expected the ostracods and leptostracans would be the most likely to respond to increasing numbers of surrounding patches of wrack in the multiple patch experiment. Leptostracans numbers were very low (1-2 individuals per sample) and had no discernible response pattern. However, ostracods did support this prediction with increasing abundances in focal patches surrounded by two and four experimental wrack patches. Ostracods occurred in the wrack and not in the underlying or bare sediment suggesting colonization occurred by individuals moving from the surrounding wrack patches. It is possible that they were able to actively locate and exploit areas with the highest levels of resource availability created, here, by the focal patches of wrack surrounded by the greatest number of similar patches.

Other taxa

Most of the taxa in the communities colonized both the wrack and material patches (*Gammaropsis* sp., *Corophium* sp., *M.senhousia*, *M.donaciformis*, and nereids), indicating a response associated with the physical structure of the wrack. Although the direction of the response by these taxa was similar to the ostracods and leptostracans the underlying mechanisms were different, that is, the ostracods and leptostracans responded to biological attributes associated with the actual wrack while the others responded to the physical structure of the wrack. Processes that may explain why these species respond to the physical structure of wrack include an escape from anoxic conditions on the sediment surface (Eriksson and Weeks 1994, Morris 2002). *Nereis diversicolor* can move freely through drift algae (Norkko et al. 2000) and has been reported to use it as a refuge when shrimp predators are present (Norkko 1998). Although bivalves are relatively less mobile than polychaetes they can still move vertically from the sediment to overlying wrack when sediment conditions are not suitable (Norkko et al. 2000), but this vertical migration is dependent on size-class and tolerance to hypoxia (Norkko et al. 2000). This may explain why we found some individuals remained in the underlying sediments, as they may be the ones that are more tolerant to

sediment changes or less mobile juveniles that may still emerge from the sediment but take longer to vertically migrate.

For the taxa in the multiple patch experiment, two different response patterns to the focal patch of wrack emerged: (1) taxa with higher abundances in the wrack compared to the controls that indicated movement of individuals from directly under the focal wrack patch and the immediate surrounding area (i.e. *Capitella* spp., *M.donaciformis*, *M.senhousia*), and (2) taxa with no difference in abundances in the wrack compared to the controls that indicated movement of individuals only from the sediment directly under the focal wrack patch (e.g. *Corophium* sp. and Nerididae).

Nerididae are generally omnivorous, eating small-bodied crustaceans and bivalves (Ronn et al. 1988) as well as microalgae and detritus in the surface layers of sediment (Nielsen and Jernakoff 1997). *Corophium* sp. are deposit feeders with high food requirements (Morris and Keough 2002) and have been recorded as prey for the nereid *Simplesetia aequistis* (Ronn et al. 1988). Although both taxa can respond quickly to changes in food availability (Norkko and Bonsdorff 1996b), it is possible that the fresh wrack deposits do not provide an immediate direct source of food (e.g. Nielsen and Jernakoff 1997) and the vertical movement we detected in our experiments was more related to changes in sediment condition (Norkko et al. 2000, Bolam and Fernandes 2002) or possibility even competitive interactions (Ronn et al. 1988).

Capitella spp., *M.donaciformis*, and *M.senhousia* are generally less mobile taxa compared to other polychaetes and amphipods found in the study and we expected them less likely to move between different wrack patches in the multiple patch experiment. Our results suggest that there was no movement of individuals between wrack patches but rather from directly underneath the wrack and from adjacent sediments. The focal wrack patches were separated from the additional surrounding patches only by 10-20 centimetres and so the movement of additional individuals must have been over very small spatial scales (i.e. < 10-20cm).

Contrary to this there was generally no effect of wrack on *Capitella* spp. in the artificial wrack experiments. Although it was one of the most abundant taxa in the artificial wrack experiment (45% of total numbers of individuals) these polychaetes generally remained in the sediments underlying the wrack and material treatments. *Capitella* spp. is the classic opportunist taxa that can have rapid population growth in the later stages of wrack decomposition when hypoxic conditions are common and competition from other taxa is low (Kelaher and Levinton 2003, Norkko et al. 2006). Prior to the formation of unfavourable sediment conditions and competitive release, *Capitella* spp. will remain in the underlying sediments but the multiple patch experiment suggest that it can, possibly only under certain conditions, play a key role in overall community response to fresh wrack deposits.

Sediment properties

The redox potential results in the artificial wrack experiment were contrary to other studies that have shown that oxygen level can deplete quickly under wrack and be as low as 20% or less of original levels within three days (Norkko et al. 2000). In the field, redox potentials under mats of green algae (*Enteromorpha* spp.) are generally lower (approximately -50 to -100 mV) than algae-free areas (~ 0 mV) (Raffaelli et al 1991). However, the porewater dissolved inorganic nitrogen under the wrack and material was high compared to the control, which indicates a shift from denitrification to the reduction of sulfate (Norkko and Bonsdorff 1996b). It is possible that wrack and material reduced the exchange of porewater and oxygen between the sediment and water during high tide, altering nutrient fluxes and denitrification processes. This also explains the redox potential as measurements ranging from +100 mV to -100 mV can be due to the reduction of other chemicals (e.g. Fe²⁺ and S), not just oxygen (Giere et al. 1988). The position of the probe in sediment in relationship to the wrack may be another explanation for these redox potential results as there can be a vertical gradient of oxygen and sulphide from algal mats into the sediment (Krause-Jensen et al 1999; Wetzel et al 2002). Dense macroalgae mats can suppress denitrification rates in the sediment but there is some indication that denitrification processes may migrate with the oxic-anoxic interface from the sediment into the lower layers of the macroalgae (Krause-Jensen et al 1999).

Conclusions

Our study shows that mobility, feeding mode and sensitivity to changes in sediment conditions are key characteristics that influence how individual taxa respond to fresh deposits of wrack on intertidal mudflats. Although the magnitude of the response was variable between sites and different times of the year the direction of the response was the same with consistent colonization of experimental patches of wrack. There were no strong changes in the composition of communities in the presence of wrack but rather a redistribution of individuals throughout the wrack-sediment habitat. In the initial stages of deposition the wrack creates an additional habitat for taxa that are mobile and able to actively select habitat niches.

The multiple patch experiment provided some insight into how the characteristics of wrack may influence community responses and compliments other studies on the effects of variable wrack deposits, specifically frequencies and intensities (Bishop and Kelaher 2007) and magnitudes (Olabarria et al. 2007). Our results suggest that the spatial arrangement of wrack is important only for taxa that are mobile and have the ability to move at that same spatial scale. These different response mechanisms could have broader implications for predicting the effects of wrack. For example, communities dominated by taxa that respond to the biological attributes of the wrack (e.g. ostracods and leptostracans) may be more sensitive to changes in factors that influence food availability and nutritional value, such as different composition of macroalgal species that make up the wrack deposits. Whereas, communities dominated by taxa that use the physical structure of the wrack as refuge from unfavourable

sediment conditions maybe more sensitive to other characteristics, such as the size of the deposit or time it persists in the habitat. .

In reality, wrack deposits are likely to have interacting components of spatial and temporal variation involving magnitude, duration, frequency and spatial arrangement and so will likely evoke numerous responses depending on mobility, feeding and perhaps even reproductive and dispersal strategies. There are now a variety of studies on wrack in marine coastal habitats and it may be possible to develop models that describe the general effects of wrack across multiple marine habitats at scales that reflect natural dynamics (Yang et al. 2010).

Wrack deposition in intertidal mudflat habitats is characterised by small patches that remain for short periods of time, creating a patchy environment of wrack in affected and non-affected areas. These events are relatively frequent and, based on our research, plays an important role in providing habitat for wrack-only taxa and a source of food or refuge from unfavourable sediment conditions that would otherwise not be present in bare sediment habitat. Wrack deposition may also be an important process for population connectivity acting as vector for dispersal of benthic invertebrate larvae (Macreadie et al. 2011). The mechanical removal of wrack is expensive and common on beaches and coastal habitats that are used recreationally (e.g. Mossbauer et al. 2012). However, the complete removal of wrack from the habitat would eliminate this resource and affect the diversity and population dynamics of the resident benthic communities. Continued research on the ecological role of wrack will assist in informing wrack removal practices and more tailored actions that could specify when wrack is removed and at what spatial and temporal scales so that biological and environmental impacts are minimised.

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Table 1: PERMANOVA results for artificial wrack experiment at Beacons Point and Kirk Point. Analyses compared community differences between treatments (C=control, PC=procedural control (Beacons Point only), M=material, and W=wrack) and experimental runs for total fauna and infauna communities. Pairwise comparisons are reported in Supplementary Table 1.

Beacons Point		Total fauna community		Infauna community	
	df	MS	P	MS	P
Treatment	3	1546	0.001	407	0.033
Run	1	735	0.0049	2315	0.001
Treat x Run	3	372	0.015	248	0.350
Residual	24	168		222	
Kirk Point		Total fauna community		Infauna community	
	df	MS	P	MS	P
Treatment	2	1217	0.0001	908	0.0053
Run	2	4259	0.0001	4847	0.0001
Treat x Run	4	767	0.0002	758	0.0031
Residual	30	163		251	

595 Table 2: Summary of results for artificial wrack experiment at **Beacons Point**. P-values > 0.05 are represented by ‘-’ and p-values < 0.05 are represented by
596 ‘+’ (actual values are in Supplementary Table 2). Planned comparisons (C = control, M = material, W = wrack) are reported instead of ‘-’ or ‘+’ when the
597 planned comparisons were < 0.05. Power was calculated for 50% change from the control to the treatments where there was no significant interaction or
598 treatment effect. ‘absent’ indicates taxa that were not present in the samples. Data was square root ($\sqrt{}$) transformed prior to analysis to improve normality and
599 homogeneity of variances (in all cases the total fauna and infauna transformations were the same).

	Total fauna				Infauna			
	Treatment	Run	Treat x Run	Power (%)	Treatment	Run	Treat x Run	Power (%)
Total individuals	-	-	-	47	-	-	-	59
Total taxa	C<(M+W)	-	-		-	-	-	91
<i>Musculista senhousia</i> ($\sqrt{}$)	-	-	-	99	C>(M+W)	-	-	
<i>Mysella donaciformis</i> ($\sqrt{}$)	-	-	-	46	-	-	-	99
Nereididae ($\sqrt{}$)	-	-	-	99	-	-	-	99
<i>Capitella</i> spp.	-	-	-	48	-	-	-	49
Spionidae ($\sqrt{}$)	-	-	-	97	-	-	-	87
<i>Corophium</i> sp. ($\sqrt{}$)	-	-	-	99	C>(M+W)	+	-	
Hydrobiidae	-	-	-	6	-	-	+	

<i>Gammaropsis</i> sp.	-	+	+	absent	absent	absent	
Ostracoda ($\sqrt[3]{}$)	M<W, C<W	-	-	absent	absent	absent	
Leptostraca ($\sqrt[3]{}$)	M<W, C<W	+	-	absent	absent	absent	
Chlorophyll	n/a	n/a	n/a	-	+	-	99
Organic content	n/a	n/a	n/a	-	+	-	99

600 Table 3. Summary of results for artificial wrack experiment at **Kirk Point**. Non-significant p-values (> 0.05) are represented by ‘-’ and p-values (< 0.05) are
601 represented by ‘+’. Planned comparisons (C = control, M = material, W = wrack) are reported instead of ‘-’ or ‘+’ when the planned comparisons were < 0.05.
602 Power was calculated for 50% change from the control to the treatments where there was no significant interaction or treatment effect. ‘absent’ indicates taxa
603 that were not present in the samples. *Redox potential and DIN were only measured for Run 3 at Kirk Point. Data was square root ($\sqrt[3]{}$) or fourth root ($\sqrt[4]{}$)
604 transformed prior to analysis to improve normality and homogeneity of variances (in all cases the total fauna and infauna transformations were the same).

Total fauna					Infauna			
	Treatment	Run	Treat x Run	Power (%)	Treatment	Run	Treat x Run	Power (%)
Total individuals	-	+	+		-	+	+	
Total taxa	-	-	Treatment in Run 3		C>(M+W)	+	-	
<i>Musculista senhousia</i> ($\sqrt[3]{}$)	-	-	+		-	-	-	11
<i>Mysella donaciformis</i> ($\sqrt[3]{}$)	-	+	-	99	-	+	-	98

Nereididae (✓✓)	C>(M+W)	+	-		C>(M+W)	+	-	
<i>Capitella</i> spp. (✓)	-	+	+		-	+	+	
Spionidae (✓)	-	-	+		-	-	+	
<i>Corophium</i> sp. (✓)	-	+	+		-	+	-	
Hydrobiidae (✓)	-	-	+		-	+	-	27
<i>Gammaropsis</i> sp. (✓)	-	+	+		-	+	-	6
Ostracoda (✓)	-	+	-	9	absent	absent	absent	
Leptostraca (✓)	-	+	+		absent	absent	absent	
Chlorophyll	n/a	n/a	n/a		-	+	-	99
Organic Content	n/a	n/a	n/a		-	+	-	99
Redox potential	n/a	n/a	n/a		C<(M+W)	n/a*	n/a	
Dissolved Inorganic Nitrogen (DIN)	n/a	n/a	n/a		C<(M+W)	n/a	n/a	

Table 4: PERMANOVA results for multiple patch experiment. Analyses compared community differences between treatments (C=control, 0W= zero, 2W=two and 4W=four wrack patches surrounding the focal patch) for total fauna and infauna only. Pairwise comparisons were between each level of treatment. Values are Monte-Carlo (MC) P-values.

	df	Total fauna community		Infauna community	
		MS	P	MS	P
Treatment	3	946	0.030	3110	0.009
Residual	12	417		1109	
		Pairwise		Pairwise	
		t	P (MC)	T	P (MC)
C v 0W		2.046	0.035	1.679	0.068
C v 2W		1.778	0.044	1.761	0.051
C v 4W		1.733	0.058	2.138	0.034
0W v 2W		0.602	0.850	0.845	0.570
0W v 4W		0.992	0.415	1.877	0.052
2W v 4W		0.623	0.790	1.460	0.128

613 Table 5. Summary of results for multiple patch experiment comparing total numbers of individuals, total taxa, numerically abundant fauna, chlorophyll and
614 organic content between treatments (sediment only). Total fauna and infauna only were analysed separately. Significant p-values ($p < 0.05$) are bold. Data
615 was square root ($\sqrt{}$) transformed prior to analysis to improve normality and homogeneity of variances (in all cases the total fauna and infauna transformations
616 were the same).

	Total fauna			Infauna		
	MS _{residual} (df=12)	p-value (df=3)	Power (%)	MS _{residual} (df=12)	p-value (df=3)	Power (%)
Total individuals	19103	0.192	6	190	0.003	-
Total taxa	1.792	0.003	-	2.504	0.083	-
<i>Musculista senhousia</i> ($\sqrt{}$)	1.339	0.892	6	0.063	0.002	-
<i>Mysella donaciformis</i>	1.254	0.040	-	17.792	0.030	-
Nereidae	0.426	0.286	34	0.281	0.197	50
Orbiniidae ($\sqrt{}$)	0.764	0.233	6	0.229	0.248	10
<i>Capitella</i> spp. ($\sqrt{}$)	23.108	0.140	97	1.944	0.015	-
<i>Corophium</i> sp.	0.374	0.791	82	0.365	0.323	84
Ostracoda* ($\sqrt{}$)	0.203	<0.001	-	-	-	-
Leptostraca* ($\sqrt{}$)	0.207	0.069	54	-	-	-

Chlorophyll a **	-	-	-	0.704	0.786	99
Organic content **	-	-	-	1.001	0.918	66

617 * not found in underlying sediment

618 ** only measured in the sediment

619

Figure captions

Figure 1. Location of Kirk Point and Beacons Point mudflats in Port Phillip Bay, Victoria, Australia.

Figure 2. Conical Analysis of Principal (CAP) ordinations of communities for the artificial wrack experiment showing differences between (a) total fauna and (b) infauna at Beacons Point, and (c) total fauna and (d) infauna at Kirk Point. Run 1 = white symbols, Run 2 = black symbols, Run 3 (Kirk Point only) = grey symbols. Control = C, procedural control = C (Beacons Point only), material = M, wrack = W.

Figure 3. Univariate analyses for artificial wrack experiment at Beacons Point in control (C), material (M) and wrack (W) treatments. Values are means + standard error (n=4) (data not transformed). Bars within each treatment represent run 1 and 2 of the experiment. Black segments within each bar represent individuals found in the wrack and white segments represent infauna (i.e. individuals found in the underlying sediment).

Figure 4. Univariate analyses for artificial wrack experiment at Kirk Point in control (C), material (M) and wrack (W) treatments. Values are means + standard error (n=4 or 5) (data not transformed). See Figure 3 caption for more details.

Figure 5. nMDS ordinations of communities for the multiple patch experiment showing differences between (a) total fauna, and (b) infauna communities. C = bare sediment control, 0W = wrack surrounded by zero additional patches, 2W = wrack surrounded by two additional patches, 4W = wrack surrounded by four additional patches.

Figure 6. Univariate analyses for the multiple patch experiment in control plots (C) and wrack treatments (0W, 2W and 4W). Values are means + standard error (n=4) (data not transformed). Black segments represent individuals found in the wrack and white segments represent infauna (i.e. individuals found in the underlying sediment).

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