

Crab-tiling reduces the diversity of estuarine infauna

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ABSTRACT: Harvesting of intertidal invertebrates for use as fishing bait is a global problem for estuary and coastal managers, with significant effects on sediments and associated infauna. Crab-tiling is a method of collection for the shore crab *Carcinus maenas*, which is then used as angling bait. This fishery operates in estuarine mudflats at a commercial scale, yet its impact on infaunal assemblages has not been quantified. The fishery involves laying hard man-made structures, known as 'crab-tiles', to attract pre-ecdysis *C. maenas*. Moulting shore crabs are harvested from underneath the tiles during low tide. Infauna surrounding these tiles, which are important prey for over-wintering wading birds and estuarine fishes, are therefore subjected to disturbance from crab-tiling activity. We experimentally manipulated sites on mudflats in 3 previously non-tiled estuaries to determine the impact of crab-tiling on macro-infaunal diversity. In addition to crab-tiled and control plots, treatments were incorporated in order to discriminate between the effects of the tiles and trampling disturbance. Response variables used were sediment penetrability, grain size and organic content as habitat-related variables, and number of taxa and abundance of individual animals as diversity estimators. The effects of crab-tiling on the sediment were contingent on the estuary; those with a greater proportion of fine particles were most affected. Simultaneously, crab-tiling reduced diversity (number of taxa and abundance of macro-infauna) and altered assemblage structure. The trampling aspect of crab-tiling was found to have the most impact on the sediment and infauna, and so crab-tiling could be managed via control of access and approaches to minimise sediment disturbance.

KEY WORDS: Bait collection · *Carcinus maenas* · Disturbance · Trampling · Anthropogenic effects

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INTRODUCTION

The harvesting of invertebrates in coastal areas for use as bait is globally widespread (Fairweather 1991, Wynberg & Branch 1991, Olive 1993), and has both direct and indirect effects on target organisms and other ecosystem components (Underwood 1993). When evaluating the sustainability of recreational fishing, there is a need to consider the effects of bait collection as well as the sustainability of fish stocks, as this component is often ignored (McPhee & Skilleter 2002, Skilleter et al. 2005).

'Crab-tiling' is a harvesting method used commercially in the UK, predominantly in the southwest

(Sheehan et al. 2008). The target organisms are pre-ecdysis shore crabs *Carcinus maenas* (L.), known locally as 'peeler crab'. Moulting crabs make excellent fishing bait for bass *Dicentrarchus labrax* (L.), plaice *Pleuronectes platessa* (L.) and other fishes. This method of bait collection involves 'crab-tilers' placing man-made materials, such as guttering, car tyres or roof tiles in intertidal habitats, in order to provide shelter for crabs.

Crab-tiled sites occupy kilometres of mudflat, depending on the available space in each estuary. The density of tiles laid, however, is generally uniform. Tiles are located in rows approximately 1 m apart, as this is believed to be the optimal spacing of tiles for

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peeler crab yield per fishing effort. The moulting threshold for *Carcinus maenas* is approximately $\geq 8^{\circ}\text{C}$ (Crothers 1968). The seawater temperature rarely drops below this in the southwest of the UK, which enables fishers to work all year round, serving their tiles every 1 to 3 d. There are approximately 77 000 'crab-tiles' laid on mudflats in the southwest UK (Black 2004). Intertidal mudflats and muddy gravels are subject to national and international levels of protection (UK Biological Action Plan, EU Annex 1 Habitats Directive). It is therefore important that the effects of crab-tiling on intertidal habitats and macro-infaunal diversity are quantified. Infauna are integral in the functioning of estuarine ecosystems (Raffaelli et al. 2003). During low water, they are prey for migratory wading birds, which use the mudflats as over-wintering feeding grounds (e.g. Goss-Custard & Verboven 1993). During high tide, infauna are eaten by ecologically and commercially important fishes, such as bass *Dicentrarchus labrax* (Kelley 1987), sole *Solea solea*, dab *Limanda limanda*, flounder *Platichthys flesus* and plaice *Pleuronectes platessa* (Costa & Elliott 1991).

Historically, the impact of bait collecting has been evaluated in terms of its impact solely on populations of the target species. For example, Blake (1979) suggested that *Arenicola marina* digging is sustainable due to the relative inefficiency of the bait diggers, but the study did not measure potential impacts on associated species. Similarly, Jackson & James (1979) found that digging for *A. marina* and *Nereis diversicolor* caused significant mortalities of the cockle *Cerastoderma edule*, but they did not record any other co-occurring fauna. More recently, the disturbance associated with bait harvesting has been found to reduce the diversity and abundance of infaunal assemblages (Nugues et al. 1996, Skilleter et al. 2006). Methods of collecting the thalassinid prawns *Callinassa kraussi* and *Upogebia africana* were found to be less detrimental to infauna than the associated indirect effects of the trampling disturbance (Wynberg & Branch 1994). As with other methods of bait collection, crab-tilers must trample sediment to service their tiles. This may adversely affect infaunal assemblages, and in addition to other types of bait collection, crab-tiling may further affect infauna due to the presence of the crab-tiles and the action of removing crabs from beneath the tiles.

Trampling can either cause sediment compaction, or it can produce thixotropic effects (increasing sediment 'gloopiness'), depending on the sediment type. Both can cause the soft-bodied fauna which live close to the sediment surface to suffer direct mortality, or indirect mortality through burial (Chandrasekara & Frid 1996). When trampling causes compaction of the sediment, available oxygen is decreased, leading to infaunal

mortality through burial, burrow collapse, or asphyxiation (Wynberg & Branch 1994, Chandrasekara & Frid 1996).

Recent work has shown that crab abundance is greater in 'tiled' estuaries than in 'non-tiled' estuaries, possibly because of extra habitat provision (Sheehan et al. 2008). Additionally, it has been suggested that crab-tiles alter the feeding behaviour of birds and provide substratum for species which are not typically found in soft sediment (Sheehan 2007). Under the model that crab-tiling affects sediment properties and infauna in mudflats, we tested the predictions that (1) sediment penetrability would be negatively affected by crab-tiling; (2) trampling would have a greater impact than tiles alone; (3) crab-tiling would alter the proportion of organic matter and the relative proportion of different grain sizes; and (4) crab-tiling would reduce biodiversity, as measured by number of taxa and number of individuals, thus modifying assemblage structure.

MATERIALS AND METHODS

Study site and experimental design. This experiment was done during July and August in the summers of 2003 and 2004, and was repeated in 3 estuaries in the southwest UK. These were the Yealm ($50^{\circ} 19' \text{N}$, $4^{\circ} 02' \text{W}$), the Erme ($50^{\circ} 19' \text{N}$, $3^{\circ} 56' \text{W}$) and the Avon ($50^{\circ} 17' \text{N}$, $3^{\circ} 52' \text{W}$). These estuaries had not previously been 'crab-tiled'. In each estuary, 6 independent sites (100 m^2) were located within a mid-shore mudflat, 3 for each year.

At each of the 3 sites, the following treatments ($n = 4$) were applied: (1) crab-tiled, in which 4 tiles (500 mm long, half-round PVC guttering) were half-inserted into the mud, sediment being cleared from below the tile before the tile was laid at a 45° angle. Tiles were serviced 3 times a week for a month, mimicking the action of crab-tiling. This entailed trampling around plots, lifting each tile in turn to remove any crabs and accumulated sediment; (2) trampling, in which areas of sediment were walked on at the same frequency and pattern as in the crab-tiling treatment but with no tiles laid; (3) tiles only, in which tiles were inserted into the sediment but otherwise not disturbed; and (4) control with neither tiles nor trampling. The comparison between (1) and (4) is of most interest for managers, whereas (2) and (3) allowed us to attribute patterns to tiles and/or trampling. Each treatment plot was 1.0 m^2 and plots were separated by 1.5 m (see Fig. 1 for a diagrammatic representation of the treatment layout).

Sample processing. Plots were sampled over 2 tidal cycles (24 h) after the final day of disturbance as follows. Samples for quantification of macrofaunal assemblages were taken using a 100 mm in diameter

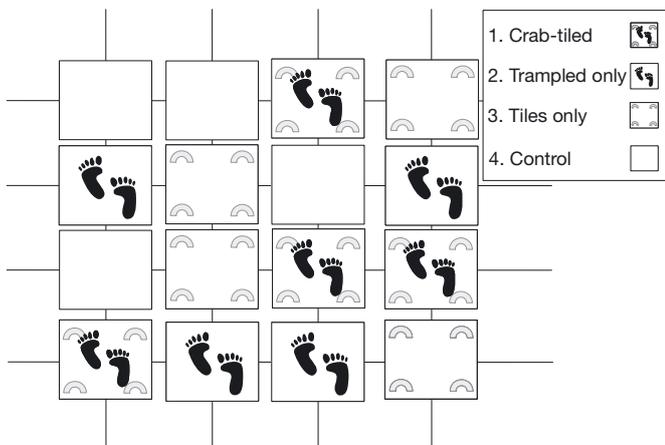


Fig. 1. The layout of treatments within a site was allocated randomly for each site and estuary

(\emptyset) \times 100 mm depth core and were then frozen. A smaller core (20 mm \emptyset \times 110 mm depth) was also taken to measure organic content and mean sediment grain size. To measure the stability of the mud, 'penetrability' of the sediment was selected as a surrogate measure using methods similar to Wynberg & Branch (1994). An iron rod (98 cm long, 1 cm \emptyset) was dropped 3 times from a standard height (20 cm) within each plot. An average of the length of rod which penetrated the sediment from the 3 replicate drops per plot was calculated.

Organic carbon content: Sediment samples were thawed then dried at 60°C for 24 h and then combusted at 450°C for a further 24 h to determine the ash-free dry weight. Organic carbon content was determined for 3 out of the 4 replicates for each treatment.

Sediment grain size: Grain size analysis was carried out for 3 out of the 4 replicates for each treatment at each site. Grain size was measured using low angle laser diffraction, with Malvern Mastersizer X (software v2. 19). Three sub-samples were taken and larger particle sizes (4 to 2000 μ m) were measured using a 1000 mm lens. Smaller particles (4 to 80 μ m) were measured using a 45 mm lens. The 2 average results were then 'blended' using a function within the software. The analysis was carried out according to ISO 13320 particle size analysis (ISO 1999). Larger fractions were put through Wentworth sieves. The final grain size parameters reported included mean grain size (Φ), sorting, % gravel, % sand and % silt.

Sub-sampling infauna trial: Smaller fauna (0.5 to 10 mm) were too abundant to pick every animal due to time constraints; therefore, a sub-sampling trial was conducted to detect what level of sub-sampling was still representative of the total sample when converted to a whole sample equivalent. Five core samples were

divided into 1/16, 1/4 and 1/2. The fauna in each section were then identified to species level where possible, and counted. These data sets were compared using the RELATE routine in PRIMER 6 to test how each subset matched the full data set. RELATE gives a ρ value: the closer ρ is to 1, the closer the match between data sets. The RELATE test indicated that a 1/2 sub-sample of the smaller fauna was the most representative of the total samples (Subset (ρ) 1/16 = 0.84; 1/4 = 0.96; 1/2 = 0.99).

Infauna identification and quantification: Samples to quantify infauna were fixed in 10% buffered formalin stained with Rose Bengal. Samples to quantify carbon content and grain size were frozen for later analysis. The 10 \times 10 cm core samples were then sieved through 0.5 mm mesh and the retained macrofauna were preserved in 70% alcohol.

Following the results of the sub-sampling trial, half of the smaller fauna (<10 mm) and all of the larger animals (\geq 10 mm) were picked from each sample. Fauna were identified and counted under a binocular or high-powered microscope as appropriate. The smaller fauna abundances were then converted to a whole sample equivalent. For the polychaetes *Nereis diversicolor* (Muller) and *Nephtys hombergii* (Savigny), small individuals have different ecological roles and different responses to disturbance than larger ones (Zwarts & Wanink 1993, Thrush et al. 2003, Rossi et al. 2007). Since the present study was concerned with ecological effects, small specimens (<10 mm) were scored separately to larger ones (>10 mm).

Data analyses. The null hypotheses of no effect of crab-tiling on sediment properties, number of macroinfaunal taxa and abundance were tested with mixed model ANOVA using the statistical software package WinGMAV 5 (Centre for Ecological Impacts of Coastal Cities EICC, University of Sydney), followed where appropriate by post hoc Student-Newman-Keuls comparisons. Factors were Year (2 levels, orthogonal and random); Estuary (3 levels, orthogonal and random); Site (3 levels, random, nested in Estuary and Year) and Treatment (4 levels: 'crab-tiling', 'trampled only', 'tiles only' and 'control'; orthogonal, fixed, $n = 4$). Hypotheses relating to the sediment particle size (Φ) and organic content were tested following the same ANOVA design, except that Treatment only had 2 levels ('crab-tiling' and 'control') and $n = 3$. Heteroscedasticity was checked using Cochran's C -test (Underwood 1997). Data which could not be transformed for heteroscedasticity were analyzed untransformed, as ANOVA is robust to heterogeneous data from relatively large, balanced experimental designs (Underwood 1997).

From a management perspective, a key aim of this study was to establish whether crab-tiling affected

infaunal diversity. In the event of complex interactions involving treatment spatio-temporal factors it is possible to count the frequency of occurrences when crab-tiling reduces diversity measures compared to control conditions. If the null hypothesis of no effect of crab-tiling is correct, then there should be an equal probability of diversity measures from crab-tiled treatments being less or greater than control measures. The null hypothesis can then be tested directly by computing the binomial probability of observing the number of occurrences of measures of diversity for crab-tiling being less than similar measures for controls (Underwood 1997). This approach tests whether the effect exists. We further tested the strength of the response (see Coleman et al. 2006) by examining the response ratio (controls/crab-tiled treatments). Providing the measures come from balanced samples, these response ratios may be used as response variables in analyses of variance (Gurevitch & Hedges 1999, Hedges et al. 1999, see Coleman et al. 2006). The response ratios were calculated from the mean of a randomly chosen pair of crab-tiling treatments per site and the mean of a randomly chosen pair of control measures per site. This gave $n = 2$ measures per site. The null hypothesis of spatial consistency of response was tested as an ANOVA using Year, Estuary and Site as factors, and heteroscedasticity was checked as before. As a further test of strength of the effect, the main response ratio was tested against a null value of zero using a 1-tailed *t*-test.

The statistical software package PRIMER (Primer-E) was used to compare infaunal assemblages (Warwick et al. 1990). Data were fourth-root transformed, and the Bray-Curtis similarity coefficient (Bray & Curtis 1957) was employed to create a similarity matrix which gives a single measure of similarity between each sample and every other. These similarities were ranked and a 2 dimensional non-metric multi-dimensional scaling (NMDS) ordination was produced. Preliminary analyses were carried out to compare samples from all 3 estuaries using a 2-factor analysis of similarities randomization test (ANOSIM, Clarke & Green 1988, Clarke et al. 1993) (Estuary \times Year). Estuaries were significantly different; therefore, all subsequent multivariate analyses were carried out separately for each estuary. Similarity matrices were recreated for each estuary and a MDS produced. An index of multivariate dispersion (IMD) calculated relative dispersion values to compare the variability of treatment samples. A 2-factor ANOSIM was used to test for differences between Treatment and Site & Year.

Pair-wise tests were used to distinguish the effects of treatment. The similarity percentages routine (SIMPER; Clarke et al. 1993, Clarke & Warwick 2001) was

used to highlight those taxa which provided the largest contribution to dissimilarity between significantly different treatments.

RESULTS

Crab-tiles were successfully harvested for crabs throughout the study period and only 3 tiles were lost. Thirty-eight taxa were recorded, most of which were identified to species level.

Sediment stability

Sediment stability (penetrability) varied between estuaries (Table 1) (mean \pm SE; Yealm 262 ± 57 mm < Erme 168.3 ± 36.9 mm and Avon 162.6 ± 26.7 mm, $p < 0.05$). Sediments in trampled treatments were consistently less stable (more penetrable) than non-trampled treatments in the Yealm and the Erme. In the Avon, 'crab-tiled' plots were more penetrable than all of the other 3 treatments. Crab-tiled sediments were therefore consistently more penetrable than those in 'controls' (Table 1, Fig. 2).

Trampling made the sediment more penetrable in the Yealm and Erme, irrespective of the presence of tiles, as plots with tiles were less penetrable than 'trampled only' plots. In the Erme, there was no significant difference between 'control' plots and 'tiles only' plots, or between 'trampled only' plots and 'crab-tiled' plots; however, treatments which were trampled ('crab-tiled' and 'trampled only') were significantly more penetrable than those which were not trampled ('tiles only' and 'control').

Table 1. Analysis of variance to test the effect of crab-tiling treatments on penetrability of the sediment, over 3 sites, in each of 3 estuaries over 2 different years. Variances were homogeneous, Cochran's $C = 0.06$, ns

Source	df	MS	F	p
Year Ye	1	20.2	2.58	0.25
Estuary Es	2	3015.5	385.08	<0.01
Treatment Tr	3	768.7	–	No test
Site Si (Ye \times Es)	12	22.9	4.09	<0.001
Ye \times Es	2	7.8	0.34	0.72
Ye \times Tr	3	10.6	1.88	0.13
Es \times Tr	6	145.7	25.95	<0.001
Ye \times Es \times Tr ^a	6	4.09		
Tr \times Si (Ye \times Es) ^a	36	5.1		
Residual	216	5.6		
Total	287			

^aTerm eliminated to increase the power of the tests above (Underwood 1997)

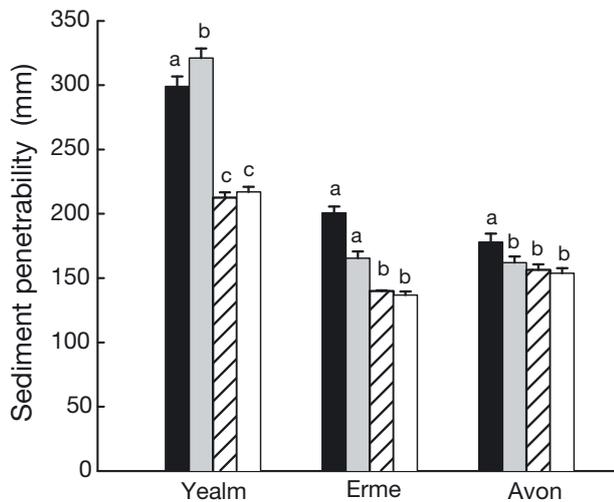


Fig. 2. Sediment penetrability (mean +SE) as a measure of sediment stability under different types of crab-tiling treatment. Treatments with the same letter were not significantly different. Black bars: crab-tiling plots (tiles, trampling and removal of crabs); light grey bars: treatments which were trampled only; hatched bars: plots which had tiles only; clear bars indicate control unmanipulated sediment

Sediment grain size

Sediments from all 3 estuaries were classified as poorly sorted sandy muds (Folk & Ward 1957). The Φ values, however, were significantly different (Table 2). The Yealm was the muddiest estuary as sites here had the highest Φ values (mean 5.8 ± 0.03 SE, i.e. lowest mean grain diameter), followed by sites in the Erme (mean 5.3 ± 0.03 SE) and then the sandiest estuary was the Avon (mean 5.9 ± 0.07 SE). Crab-tiling, however, had no effect on sediment particle size (Table 2).

Table 2. Analysis of variance to test the effect of crab-tiling treatment on organic content (variances were homogeneous, Cochran's $C = 0.17$, ns) and mean grain diameter, Φ (variances were heterogeneous, $C = 0.8$, $p < 0.01$), at 2 different spatial scales (Site and Estuary)

Source	df	Organics (%)			Φ		
		MS	F	p	MS	F	p
Year Ye	1	124.6	46.17	<0.001	0.011	1.49	0.2451
Estuary Es	2	37.3	13.81	<0.001	0.262	33.97	<0.001
Treatment Tr	1	2.6	1.2	0.39	0.002	0.33	0.57
Site (Ye \times Es)	12	2.7	3.54	<0.001	0.008	1.69	0.09
Ye \times Es	2	0.3	a	a	0.002	a	a
Ye \times Tr	1	0.02	a	a	0	a	a
Es \times Tr	2	2.5	a	a	0.003	a	a
Ye \times Es \times Tr	2	2.2	1.98	0.18	0.002	a	a
Tr \times Si (Ye \times Es)	12	1.1	1.43	0.17	0.005	a	a
Residual	72	0.8			0.005		

^aTerm eliminated to increase power of tests above (Underwood 1997)

Organic content

The organic content of the sediment differed between Sites, Estuaries and Years but was unaffected by crab-tiling (Table 2).

Macro-infaunal diversity

Number of taxa and abundance

The magnitude of the treatment effect varied at small spatial scales for each year: the term Treatment \times Site (Estuary \times Year) was significant for 'number of taxa' (Table 3, Fig. 3) and 'abundance' (Table 3, Fig. 4). There was no apparent pattern for 'trampled only' or 'tiles only' treatments but in 13 out of 18 possible combinations the 'number of taxa' were less in 'crab-tiling' treatments than in 'controls' (binomial probability, $p < 0.05$). The same was true for 'abundance' of infauna (15 out of a possible 18 trials, $p < 0.01$). Thus, it is logical to examine the response ratio as a measure of the strength of the effect. The null hypothesis of spatial consistency in the effect of crab-tiling was retained in that the response ratio did not vary across Sites, Estuaries or Years (Table 4). The null hypothesis that the effect was small, i.e. that the mean response ratio was similar to zero, was rejected ($n = 36$, 1-tailed t -test: Number of taxa $t_{35} = 2.32$, $p < 0.05$; Abundance $t_{35} = 4.01$, $p < 0.001$).

Infaunal assemblages

Multivariate analysis showed that infaunal assemblages were significantly different between estuaries and years (Fig. 5; ANOSIM Estuary: $R = 0.77$, $p < 0.02$; Year: $R = 0.41$, $p < 0.02$). The location of the symbols indicated that assemblages were more dissimilar between estuaries than years. ANOSIM can only compare a maximum of 2 factors at a time; therefore subsequent analyses consider each estuary separately.

MDS ordinations for the muddiest estuaries, the Yealm and the Erme, show a clear distinction between those treatments which were trampled ('crab-tiling' and 'trampled only') and those which were not ('tiles only' and 'control') (Fig. 6). Also, while the 'control' and the 'tiles only' plots were relatively tightly clustered, the 'crab-tiling' and the 'trampled only' treatments were more dispersed (Table 5). ANOSIM detected a significant

Table 3. Variation in diversity of macro-infauna under different crab-tiling treatments in 3 sites over 2 years. Heteroscedasticity was tested by Cochran's *C*. Number of taxa, (variances were homogeneous, *C* = 0.05, ns), and abundance (variances were homogeneous, *C* = 0.09, ns)

Source	df	Number of taxa			Abundance		
		MS	<i>F</i>	<i>p</i>	MS	<i>F</i>	<i>p</i>
Year Ye	1	25.09	15.4	0.06	51.37	4.80	0.16
Estuary Es	2	106.3	65.3	<0.05	4.59	0.43	0.7
Treatment Tr	3	32.59	–	No test	9.33	–	No test
Site (Ye × Es)	12	19.28	4.81	<0.001	5.43	10.43	< 0.001
Ye × Es	2	1.63	0.08	0.92	10.71	1.97	0.18
Ye × Tr	3	4.58	1.31	0.35	1.11	0.64	0.61
Es × Tr	6	9.05	2.59	0.14	1.74	1.00	0.5
Ye × Es × Tr	6	3.49	0.57	0.75	1.74	1.63	0.16
Tr × Si (Ye × Es)	36	6.09	1.52	<0.05	1.07	2.05	< 0.001
Residual	216	4.01			0.52		

treatment effect and a significant Year and Site effect (Table 6). Subsequent pair-wise tests showed that infaunal assemblages were only significantly different between samples when a treatment with trampling was compared to a treatment without trampling. The presence of tiles alone did not influence infaunal assemblages.

In the less muddy Avon estuary, the composition of infaunal assemblages was not affected by crab-tiling; however, assemblages did vary depending on the year or site (Fig. 6). All of the symbols from Year 1 were located on one side of the ordination, while all those on the other

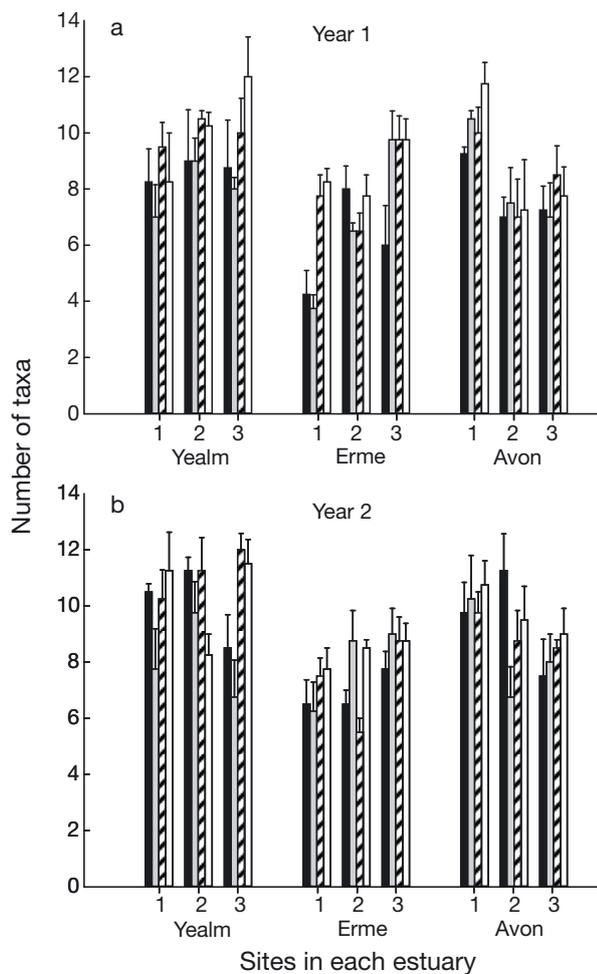


Fig. 3. Number of taxa (mean +SE) of macro-infauna at each site in each estuary for different levels of the crab-tiling treatment. Data for (a) 2003 and (b) 2004. Black bars: crab-tiling plots (tiles, trampling and removal of crabs); light grey bars: treatments which were trampled only; hatched bars: plots which had tiles only; clear bars control unmanipulated sediment

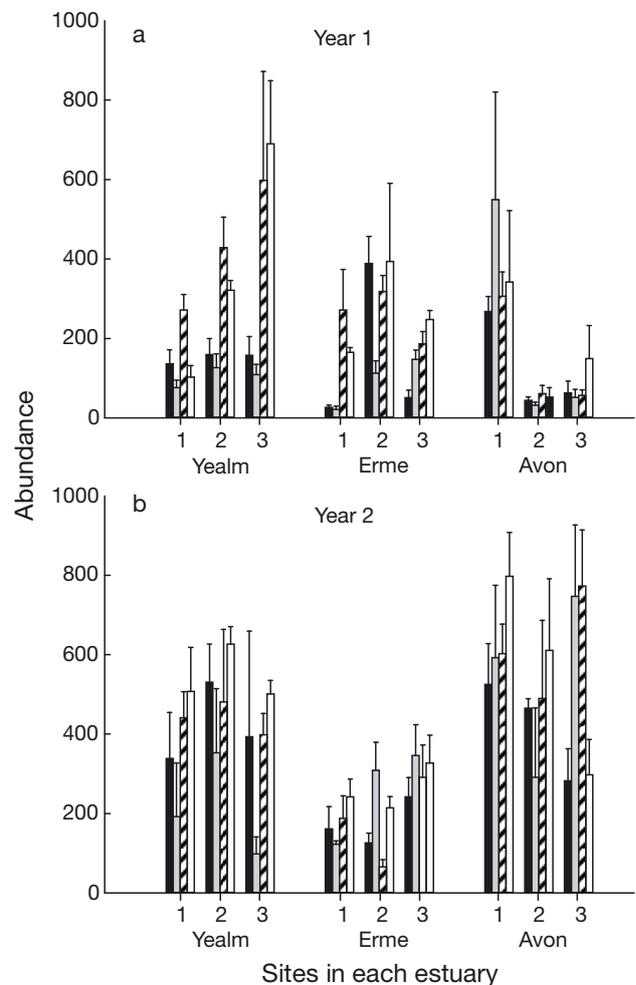


Fig. 4. Abundance (mean +SE) of macro-infauna at each site in each estuary for different levels of the crab-tiling treatment. Data for (a) 2003 and (b) 2004. Black bars: crab-tiling plots (tiles, trampling and removal of crabs); light grey bars: treatments which were trampled only; hatched bars: plots which had tiles only; clear bars: control unmanipulated sediment

Table 4. Variation in the response ratio as a measure of effect size for crab-tiling over Years (2003 and 2004), Estuaries (Yealm, Erme and Avon) and Sites (1 to 3). Cochran's C was used to check heteroscedasticity. Number of taxa (variances were homogeneous, $C = 0.23$, ns) and abundance (variances were homogeneous, $C = 0.23$, ns)

Source	df	Number of taxa			Abundance		
		MS	F	p	MS	F	p
Year Ye	1	0.03	0.35	0.62	0.84	2.41	0.26
Estuary Es	2	0.28	3.73	0.21	1.09	3.13	0.24
Ye \times Es	2	0.08	0.76	0.49	0.35	0.49	0.62
Site (Ye \times Es)	12	0.1	2.34	0.05	0.7	1.41	0.25
Residual	18	0.04			0.5		

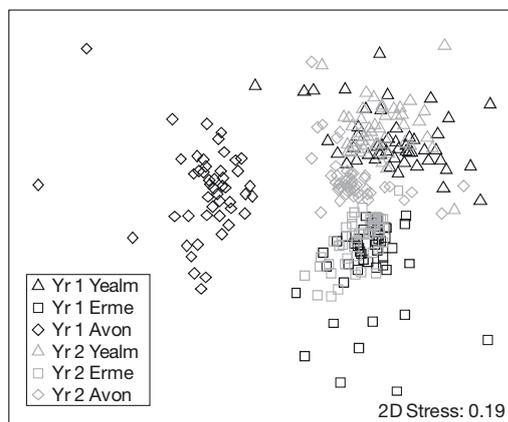


Fig. 5. Non-metric multi-dimensional scaling (NMDS) ordination demonstrating the dissimilarities of infaunal assemblages between estuaries and between years (Yr 1 = 2003, Yr 2 = 2004)

side were from Year 2. Samples from all 4 treatments ('crab-tilled', 'trampled only', 'tiles only', and 'control') were all similarly dispersed (IMD, Table 5) and showed no patterns of clustering within treatment (MDS, Fig. 6). The effects of Year and Site were stronger than any disturbance effect resulting from experimental treatments (ANOSIM, Table 6).

In the Yealm, the oligochaetes *Tubificoides benedii* (Udekem), *T. pseudogaster* (Dahl) and *Paranais litoralis* (Müller) contributed most to the dissimilarity between treatments, and were all more abundant in non-trampled treatments than trampled treatments, contributing 21.4 % of the dissimilarity between treatments (Appendix 1). Small polychaetes, Spionidae spp., the sabellid worm *Manayunkia aestuarina* (Bourne), large polychaete *Nephtys hombergii*, gastropod *Hydrobia ulvae* (Pennant), bivalve *Macoma balthica* (L.) and shrimp *Crangon crangon* (L.) were also found in greater abundance in non-trampled plots than in those which were trampled. Conversely, the polychaete *Capitella*

capitata (Fabricius), nematodes and the crab *Carcinus maenas* were more abundant in the trampled treatments than the non-trampled treatments.

Of the fauna in the Erme which contributed at least 1% of the dissimilarity between treatments, only 2 species were found in greater abundance in the trampled treatments: the bivalve *Scrobicularia plana* (da Costa) and the crab *Carcinus maenas* (Appendix 1). All other fauna were more abundant in non-trampled treatments, including the oligochaetes *Tubificoides benedii*, *T. pseudogaster*, *Heterochaeta costata* (Claparède) and

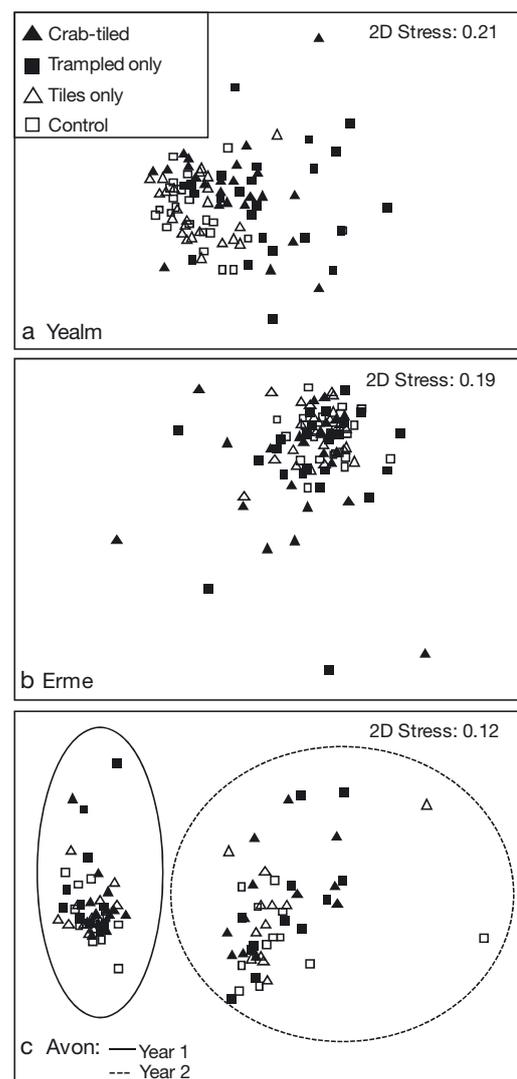


Fig. 6. Ordination displaying dissimilarities of infaunal assemblages between treatments in the (a) Yealm, (b) Erme and (c) Avon

Table 5. Index of multivariate dispersion (IMD) for each treatment ('crab-tiled', 'trampled only', 'tiles only' and 'control') in each estuary (Yealm, Erme and Avon)

	Yealm	Dispersion Erme	Avon
Control	0.837	0.747	0.976
Tiles only	0.773	0.768	0.958
Trampled only	1.348	1.222	1.115
Crab-tiled	1.042	1.263	0.951

Table 6. Two-way crossed ANOSIM test for Treatment and Year & Site on fourth root-transformed infaunal assemblage data in each estuary (Yealm, Erme and Avon). Treatments are: 'crab-tiled' (CT), 'trampled only' (Tr), 'tiles only' (Ti) and 'control' (C). Years: 2003 and 2004; Sites: Sites 1, 2 and 3. **Bold** indicates significant comparisons

	Yealm		Erme		Avon	
	R	p	R	p	R	p
ANOSIM						
Treatment	0.15	0.002	0.15	0.001	−0.01	0.598
Year & Site	0.22	0.001	0.35	0.001	0.63	0.001
Pairwise tests for treatment						
C, Ti	−0.01	0.55	0.08	0.14	−0.1	0.96
C, Tr	0.31	0.001	0.13	0.02	0.03	0.33
C, CT	0.25	0.001	0.22	0.001	0.11	0.05
Ti, Tr	0.28	0.001	0.23	0.001	−0.08	0.88
Ti, CT	0.16	0.02	0.19	0.003	0.01	0.46
Tr, CT	−0.03	0.67	0.11	0.08	0.03	0.3

Paranais litoralis, which were responsible for nearly 30% of the dissimilarity between treatments, and the polychaetes Spionidae spp., *Nereis diversicolor*, *Manayunkia aestuarina*, *Capitella capitata*, which contributed to 34.7% of the dissimilarity. The gastropod *Hydrobia ulvae* and Nematoda were also important in the dissimilarity between treatments.

Despite the infaunal assemblages not being significantly different between treatments in the Avon, similar trends were evident to those in the Yealm and the Erme. Out of the 20 taxa which each contributed at least 1% of the variation between treatments, only 4 species were more abundant in the trampled treatments than the non-trampled treatments, and of those, 2 were surface feeders, *Carcinus maenas* and *Hydrobia ulvae* (Appendix 1), which are unlikely to be affected by sediment disturbance in the same way as the infaunal taxa.

DISCUSSION

Crab-tiling is a relatively understudied and comparatively unregulated fishery. Here we present experimental evidence of a negative impact of crab-tiling on

macro-infaunal estuarine diversity with simultaneous effects on sediment properties.

The hypothesis that crab-tiling modifies sediment stability measured by penetrability was supported. It appeared as if this effect was probably caused by trampling, although the extent of change was influenced by relatively small changes in the sediment composition in the studied estuaries. There was no effect of crab-tiling on either organic content or grain size, with existing differences due to among-estuary variation masking any other patterns. While there was much spatial and temporal variation in the effect of the different treatments on number of taxa and abundance of macro-infauna, when only the comparison of crab-tiling versus controls was considered, there was sufficient evidence to retain the hypothesis that crab-tiling reduces measures of diversity.

Infaunal diversity and abundance are known to be directly influenced by sedimentary factors (Gray 1974, Rhoads 1974, Warwick et al. 1990). In general, mean abundance per treatment declined with increasing mean penetrability of the sediment, used in this study as a surrogate for sediment stability. For example, in the Yealm, 'controls' and 'tiles only' had a similar measure of sediment stability and similar abundance to each other, while sediments in 'trampling only' treatments were least stable and had the lowest infaunal abundance. In addition, 'crab-tiled' plots, which were more stable than 'trampling only' plots, also had greater abundance. This pattern of association was consistent for each estuary. The depth of the trampling effect (300 to 500 mm) in this study was deeper than that noted previously (Cook et al. 2002). This suggests that trampling was the mechanism that contributed most to the decrease in infaunal abundance rather than the insertion of the tiles. This association could be due to the mortality of individuals from the direct effect of trampling, or indirectly through burial (Chandrasekara & Frid 1996, Rossi et al. 2007). Species may also have avoided trampled sediment, decreasing immigration to the area, and/or may have increased the number of organisms leaving the area (emigration) (Negrello Filho et al. 2006). Increased trampling intensity has been directly related to the damage of flora in terrestrial assemblages (Bayfield 1979, Cole 1995), the extent of disturbance of salt marsh infauna in vegetated and unvegetated areas (Chandrasekara & Frid 1996), the densities and diversities of algae and sessile organisms on rocky shores (Keough & Quinn 1998) and the amount of direct breakages to coral reefs and/or mortality of coral colonies (Hawkins & Roberts 1993).

Infaunal assemblages differed most (Warwick & Clarke 1993) between those sampled in the controls and those in crab-tiling treatments in the muddiest estuaries (Yealm and Erme), while in the sandiest estuary (Avon), no significant treatment effects on infaunal assemblages were detected. Nevertheless, 16 out of the

21 taxa in the Avon were more abundant in the non-trampled treatments than the trampled treatments. The Avon was sandier, and thus less penetrable and less susceptible to disturbance caused by trampling.

In the Yealm and the Erme, infaunal assemblages differed depending on whether the treatment was trampled or non-trampled. Therefore, 'control' plots and 'tiles only' plots were more similar, as were 'crab-tiled' and 'trampled only' plots. Most taxa were more abundant in the non-trampled treatment. Evidence from SIMPER analyses suggests that the disturbance caused to infauna from crab-tiling varied according to species and could be spatially variable. Differences observed in the abundance of certain species may be related to the effect that crab-tiling had on the surface rugosity of the sediment. Pits and troughs in sediment have been found to increase variation in the abundance of crustaceans (McLusky et al. 1983) and polychaetes (Longbottom 1970). This pattern has been attributed to the accumulation of organic matter (Longbottom 1970); however, there was no difference in organic content among treatments in this study. The grain size measurement Φ was not affected by crab-tiling when measurements were taken between tiles. The tiles themselves may, however, have caused finer sediment particles to accumulate beneath them, which was observed with intertidal oyster trestles on muddy sandflats in the Exe Estuary, southwest UK (Nugues et al. 1996).

Other types of intertidal harvesting are also known to impact infaunal abundance and diversity. Nugues et al. (1996) found intertidal oyster cultivation to significantly decrease the diversity and abundance of benthic fauna. Skilleter et al. (2006) found that bait harvesting for bloodworms *Marphysa* spp. also negatively impacted benthic fauna, including gammarid amphipods, polychaetes and gastropods. Two studies have reported different levels of impact to infauna from the effects of harvesting callinassid shrimp. Wynberg & Branch (1997) found that the effects of trampling while bait harvesting caused a significant reduction to infauna abundance, but did not affect diversity, while Skilleter et al. (2005), using mensurative and manipulative experiments, found that bait harvesting neither affected number of taxa nor individuals. This demonstrates the difficulty of extrapolating from other systems when attempting to utilise evidence based management of bait collection in sedimentary systems.

Potential effects of crab-tiling on ecosystem functioning

Disturbed sediments often support fewer species but greater numbers of individuals than undisturbed sediments (Clarke & Warwick 1994). In contrast, in the pre-

sent study, the number of macro-faunal taxa and their abundance were lower in disturbed plots than in control plots. As the experiment only ran for 1 mo, there may not have been time for the abundance of opportunistic species that are more tolerant to disturbance to increase.

Infauna play a significant role in the ecosystem functioning of estuaries. Ecologically, it is important to determine the effects of crab-tiling on infaunal assemblages, due to the extent of crab-tiling in estuaries in the southwest UK. These estuaries are important feeding grounds for fishes of commercial and conservation importance (Elliott & Taylor 1989, Marshall & Elliott 1997), and for migrating wading shorebirds (Goss-Custard & Verboven 1993). A decrease in overall abundance would entail a decrease in the potential food supply for such species (Zwarts & Wanink 1993). Infauna also provide a further ecological function as bioturbators (Biles et al. 2002). Some bioturbators have an important influence on sediment characteristics making it more habitable for other species (Gallagher et al. 1983, Wynberg & Branch 1994, Schlacher & Wooldridge 1996). For example, the present study found that Spionidae occurred in lower abundances in the trampled treatments than the non-trampled treatments in all 3 estuaries sampled. This family is important in structuring co-occurring infaunal assemblages, as their tubes in the sediment facilitate the settlement of other fauna (Gallagher et al. 1983). Also, a reduction in the number of bioturbators could lead to 'functional extinction' of fauna, making some species effectively unable to contribute to ecosystem processes (Dayton et al. 1998); for example, by decreasing the direct release of nutrients into the water column through the oxygenation of the sediment and particle erosion (Cadée 1976, Brenchley 1981, Falcão et al. 2006). In order to test this model, further laboratory and field manipulative experiments would be required.

The magnitude of any of these previously discussed effects could be further modified depending on species body size and density (Thrush et al. 2003). Physical activities of crab-tiling were found to have different magnitudes of effect on cohorts of the same species. In the Yealm, crab-tiling had a greater effect on adult *Nephtys hombergii*, which were 32% less abundant in tiled plots than control plots, whereas in the Erme, juvenile *Nephtys hombergii* were only 19% less abundant in tiled plots. Smaller animals may be less profitable as prey items than larger fauna, providing larger animals do not require a significantly longer handling time. Also, larger animals are more significant burrowers. Adult *Nereis diversicolor* occasionally construct deep U-shaped burrows, which they irrigate through undulating their bodies laterally (Christensen et al. 2000), thereby promoting deeper layers of the sediment to be oxygenated and stimulating both nitrification and denitrification.

Management relevance and recommendations for policy

This study has shown that crab-tiling simultaneously modified sediment stability and measures of infaunal diversity. The results indicate that muddy estuaries will be more susceptible to disturbance caused by crab-tiling than sandy ones. Since muddy estuaries are important feeding and nursery areas for ecologically and commercially important fishes (Marshall & Elliott 1997, Elliott & Taylor 1989) and birds (Goss-Custard and Verboven 1993), we propose that efforts be made to reduce crab-tiling in muddy estuaries and to direct new crab-tiling activities to sandier estuaries. Since it is likely that trampling is a major contributor to the effects noted, we suggest that semi-permanent walkways be utilised. It is possible that site rotation may also be a suitable strategy, but initial tests (E. V. Sheehan unpubl. data) suggest this may not be viable.

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Appendix 1. SIMPER 2-way analysis in the Yealm, Erme and Avon sites (Treatment × Site and Year) to compare the combined abundances of infauna for treatments 'control' (C) and 'tiles only' (Ti) with the combined abundances of infauna for treatments 'crab-tiled' (CT) and 'trampled only' (Tr). Diss: dissimilarity between treatments. **Bold**: set of treatments with the greatest abundance of individuals

Species	Mean abundance		Diss/SD	% contribution to diss
	C and Ti	Tr and CT		
Yealm (average dissimilarity = 40.36)				
<i>Tubificoides pseudogaster</i>	2.29	1.40	1.08	8.26
<i>Capitella capitata</i>	0.74	1.29	1.07	7.60
Spionidae spp.	3.18	2.22	1.43	7.59
<i>Tubificoides benedii</i>	3.57	2.88	1.22	7.56
<i>Manayunkia aestuarina</i>	1.77	1.17	1.18	7.25
Chironomidae larvae	1.05	0.29	1.23	6.51

Appendix 1 (continued)

Species	Mean abundance		Diss/SD	% contribution to diss
	C and Ti	Tr and CT		
Yealm (continued)				
<i>Hydrobia ulvae</i>	1.02	1.11	1.04	5.67
<i>Paranais litoralis</i>	0.89	0.53	0.87	5.53
<i>Nereis diversicolor</i> juv.	0.83	0.42	1.05	5.27
Nematoda spp.	0.78	0.90	1.04	5.25
<i>Nephtys hombergii</i>	1.48	1.01	0.97	4.66
Copepoda (Harpacticoida)	0.67	0.63	0.87	4.63
<i>Macoma balthica</i>	0.56	0.14	0.83	3.64
Cirratulidae spp.	0.43	0.28	0.80	3.62
<i>Melinna cristata</i>	0.46	0.08	0.81	3.28
<i>Nephtys hombergii</i> juv.	0.32	0.26	0.61	2.39
<i>Carcinus maenas</i>	0.28	0.12	0.60	2.35
<i>Crangon crangon</i>	0	0.25	0.52	1.83
<i>Cerastoderma edule</i>	0.14	0.14	0.52	1.78
<i>Mytilus edulis</i>	0.12	0.16	0.48	1.74
Enchytraeidae spp.	0.11	0.02	0.28	1.02
Erme (average dissimilarity = 33.85)				
<i>Tubificoides pseudogaster</i>	2.79	2.40	0.96	10.30
Spionidae spp.	1.50	1.05	1.15	9.93
<i>Heterochaeta costata</i>	1.72	1.35	0.88	9.29
<i>Tubificoides benedii</i>	1.72	1.45	1.08	8.49
<i>Nereis diversicolor</i> juv.	2.50	1.87	1.05	8.45
<i>Hydrobia ulvae</i>	1.57	1.49	1.10	8.04
<i>Nereis diversicolor</i>	1.87	1.47	0.81	7.48
<i>Manayunkia aestuarina</i>	0.93	0.71	1.03	7.22
Nematoda	0.66	0.59	1.09	7.19
<i>Macoma balthica</i>	0.76	0.58	0.96	6.60
<i>Cyathura carinata</i>	0.39	0.37	0.74	4.28
Tipulidae spp.	0.26	0.12	0.60	2.95
<i>Scrobicularia plana</i>	0.13	0.18	0.54	2.42
<i>Paranais litoralis</i>	0.11	0.08	0.40	1.73
<i>Capitella capitata</i>	0.11	0.08	0.39	1.58
<i>Carcinus maenas</i>	0.05	0.11	0.39	1.53
Avon (average dissimilarity = 33.85)^a				
<i>Paranais litoralis</i>	1.73	1.66	0.99	9.49
<i>Tubificoides pseudogaster</i>	2.58	2.66	0.91	9.37
<i>Nereis diversicolor</i> juv.	1.35	0.91	1.04	8.91
<i>Capitella capitata</i>	1.63	1.30	0.91	8.22
<i>Hydrobia ulvae</i>	0.60	0.70	0.90	6.99
<i>Tubificoides benedii</i>	2.06	2.04	0.73	5.94
<i>Omalogyra atomus</i>	0.42	0.45	0.61	5.33
<i>Melinna cristata</i>	0.57	0.51	0.56	5.24
<i>Cerastoderma edule</i>	0.44	0.36	0.64	4.91
<i>Ampharete acutifrons</i>	0.52	0.52	0.56	4.47
Spionidae spp.	1.00	0.95	0.60	3.83
<i>Manayunkia aestuarina</i>	0.54	0.44	0.60	3.15
Nematoda	1.27	1.16	0.62	3.03
<i>Heterochaeta costata</i>	0.77	0.67	0.55	2.87
<i>Macoma balthica</i>	0.33	0.15	0.57	2.79
Enchytraeidae spp.	0.39	0.33	0.43	2.46
<i>Nereis diversicolor</i>	0.77	0.59	0.54	2.40
<i>Mytilus edulis</i>	0.23	0.19	0.56	2.33
<i>Dodecaceria concharum</i>	0.07	0.05	0.32	1.39
Cirratulidae spp.	0.11	0.08	0.34	1.28
<i>Carcinus maenas</i>	0.02	0.14	0.36	1.22

^aIncluding only those species which contributed over 1% of the dissimilarity between treatments