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Recovery of meiofauna communities following mudflat
disturbance by trampling associated with crab-tiling

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Abstract

The provision of artificial shelters for the collection of crabs, known as crab-tiling, and the subsequent harvesting of the soft “peeler” crabs for angling bait, are associated with trampling disturbance of intertidal mudflats in the United Kingdom. Recovery of meiofauna communities following crab-tiling activity was investigated on an intertidal mudflat in SW England. Harvesting of experimental plots was reproduced 6 times over a 2-week period. Meiofauna was collected at low tides 12 h, 36 h and 144 h after treatment. Meiofaunal and nematode abundance, and nematode species number, was significantly greater in controls compared to crab-tile stations at 12 h. At 36 and 144 h there were no significant differences between treatments, indicating recovery had occurred in 12-36 h. Multivariate analysis showed nematode assemblage composition from control plots to be significantly different from crab tile plots at 12 h. No significant differences were observed between sediment physical parameters with treatment. Results suggest that the predominant effect of disturbance may be vibration-induced burial, which causes nematodes to bury deeper into the sediment, beyond the depth sampled, and explains the rapid recovery.

KEY WORDS: Meiofauna, Recovery, Crab-tiling, Disturbance, Nematodes

1. Introduction

Collection of bait for anglers is a common practice along many UK shores (Fowler, 1999). Prior to moulting, green shore crabs (*Carcinus maenas* L.) have soft shells and are known as 'peelers' or 'softbacks' (Cook et al., 2002). They seek refuge under structures on the shore because of their vulnerable state. Peeler crabs are believed to release pheromones which attract fish, making them popular as bait. Crab-tiling involves the placement of structures along foreshores of estuaries under which moulting *C. maenas* seek shelter, making it easy to harvest them at low tide. Crab tiles can be materials such as concrete roofing tiles laid on the sediment or pieces of plastic guttering inserted into the sediment.

With an increase in sea angling in the UK in recent years there has been a subsequent increase in demand for good bait, leading to an expansion in the use of artificial shelters to increase crab catches on soft sediment shores. The increased deployment of artificial shelters has led to concerns about possible impacts on crab populations and estuarine ecosystems (Fowler, 1999). There is particular worry because intertidal flats and saltmarshes are important components of coastal systems, providing food for many commercially important populations of invertebrates, fish and, in particular, birds (Ray, 2000). Crab-tiling has the potential to affect estuarine ecosystems in a number of ways: direct mortality to benthos may be caused by operator trampling (Chandrasekara and Frid, 1996; Wynberg and Branch, 1997); crab stocks may be depleted (Cook et al., 2002); placement of tiles could disturb sediment and alter bed topography and hydrodynamics (Young and Southard, 1978; Thrush et al., 1992); increased crab populations on small spatial and temporal scales may increase predation and bioturbation (Schratzberger and Warwick 1999); and

trampling of sediment during collection might alter habitat characteristics (Brosnan and Crumrine, 1994).

Meiofaunal organisms are highly abundant in intertidal sediments. They are characterised by direct benthic development, with the whole of their life-cycle closely coupled to the sediment, no specific dispersal phase, and generation times very much less than one year. Free-living nematodes are the numerically dominant group of Metazoa in the majority of marine sediment ecosystems. Warwick (1988) and colleagues (Heip et al., 1988) hypothesised that aspects of their ecology might make them more sensitive to rapid changes in the environment, compared to the majority of macrofaunal organisms which often live for more than a year, and often have a planktonic phase in their life-cycle. It was further hypothesised (Warwick et al., 1990) that meiofauna are less sensitive to physical disturbance than macrofauna. This was followed up by experimental studies (Schratzberger and Warwick, 1998; 1999) which demonstrated, *inter alia*, that nematodes are sensitive to the nature, frequency and quantity of disturbance, but that different assemblages may be predisposed to disturbance.

We undertook a field experiment to determine: the effects of crab-tiling activity on nematode assemblages within an estuarine mudflat typical of those generally used for bait collection in SW England and, specifically to determine the time required for nematode assemblages to recover from associated disturbance.

2. Materials and methods

Experimental plots were assembled on a tidal flat at Shortafleet Creek in the Yealm Estuary, Devon, S.W. England (Fig. 1). Two grids, 10 m x 10 m, were

constructed 40 m from each other at the same tidal height. Grids were divided into 1 m² plots that were randomly allocated treatments: control plots (n = 8) were left untouched for the course of the experiment; guttered and trampled plots (n = 8) had plastic guttering inserted into the sediment at each corner and were then subjected to trampling 6 times over a 2-week period. Trampling was undertaken in a manner to simulate the movement of operators collecting crabs from under tiles.

Samples were taken 12, 36 and 144 h after the last trampling. 2 replicates of each treatment were taken from each grid on each sampling occasion. Meiofauna was sampled to a depth of 11 cm using a 2 cm-diameter core with a resulting volume of 34.6 cm³, and then fixed in 10 % formalin. Sediment was collected for analysis using a 5 cm diameter core to a depth of 11 cm. In each sampled plot, penetrability of the sediment (i.e. how firmly packed it is) was measured by dropping a 1 m iron rod from a height of 20 cm and measuring its penetration into the sediment (Wynberg and Branch, 1994); the average of three replicates was calculated.

In the laboratory, meiofaunal extraction and mounting methods followed Somerfield and Warwick (1996) and Somerfield et al. (2005). Briefly, cores were washed through a 500 µm sieve overlying a 63 µm sieve to remove formalin and larger sediment particles, and the fauna extracted by flotation using Ludox-TM with a specific gravity of 1.15. 5 % sub-samples were taken and washed into cavity blocks using a mixture of 5 % glycerol and 10 % ethanol. The cavity blocks were left on a warm hotplate overnight to evaporate to pure glycerol. Material from each sample was transferred to a prepared microscope slide with a rectangular paraffin wax ring. A coverslip was added over the wax ring, which was carefully melted to seal the slide, and the preparation was ringed with Bioseal No. 2 mountant. Meiofauna was counted and identified under a compound microscope with conventional bright-field

illumination. Nematodes were identified to species, or putative species, using appropriate keys (Platt and Warwick, 1983; 1988; Warwick et al., 1997).

A Malvern Long-bed Mastersizer X laser particle sizer was used to analyse sediment grain size. Three subsamples were taken and larger particle sizes (4-2000 μm) were measured using a 1000 mm lens. Smaller (0.1-80 μm) particles were analysed in a fourth subsample using a 45 mm lens. For organic-matter determination, sediment samples were dried at 60 °C for 24 h, weighed, combusted at 450 °C for 24 h, and reweighed to determine ash-free dry weight.

For univariate statistical analyses, normality and homogeneity of variances were determined using Anderson-Darling's and Cochran's tests and, where appropriate, transformations ($\ln(x+1)$) applied. All analyses between plots for each time period were found to be non-significant (all $F_{1,8} < 3.31$, all $p > 0.143$), so to allow for a more powerful test, data were pooled and analyses consisted of a series of 1-way ANOVA tests (treatment at each time period). Formal 2-way ANOVA was not considered appropriate as time periods needed to be considered separately to determine when recovery was complete; the time periods are not true replicates as the assumptions about differences will vary with time (and thus hypotheses). Additionally, 2-way analysis in this context would rely primarily on post-hoc pairwise tests to assess differences within time-treatment interactions. Due to the comparatively low power of such an approach (in respect to ANOVA), this method increases the chances of Type II errors. All univariate analyses were conducted using MINITAB 13.

PRIMER 6 was used for non-parametric multivariate analyses (Clarke, 1993; Clarke and Gorley, 2006). Nematode abundances were dispersion-weighted to downweight contributions to intersample similarities from species with significant overdispersion (Clarke et al., 2006a). Intersample similarities were calculated using

an adjusted form of the Bray-Curtis similarity coefficient (Clarke et al., 2006b) as some samples contained very low abundances and it could be assumed that these were depauperate for similar reasons. Intersample similarities were ordinated using non-metric multidimensional scaling (MDS). Environmental variables were normalised (by subtracting the mean and dividing by the standard deviation) to convert them to a standard scale, and dissimilarities between samples calculated using Euclidean distance (Clarke et al., 2006b). Formal significance tests for differences between groups of samples were addressed using ANOSIM (analysis of similarity) permutation tests. A series of 1-way tests were used to test for differences between treatments at different times, following the logic of the ANOVA analyses. Species contributing to dissimilarities between groups of samples were examined using the similarities percentage (SIMPER) procedure (Clarke, 1993).

3. Results

In higher-way analyses of abiotic and biotic data, there were no significant differences (all $p > 0.05$) between grids, and samples were treated as replicates for subsequent analyses. Differences in abiotic factors (grain size, total organic content and penetrability) between control and crab-tile plots were not significant at any time during the experiment; multivariate analyses indicated no effect of treatment or time (ANOSIM Global $R = 0.066$, $p = 0.185$).

Nematoda was the dominant meiofaunal taxon in the mudflat, comprising 83.1 % of individuals on average and accounting for up to 100 % in some samples. Copepoda contributed 17.7% of the meiofauna on average, while small numbers ($< 3 \text{ cm}^{-3}$) of Polychaeta, Ostracoda, Acari, Oligochaeta and Kinorhyncha made up the

rest. Meiofaunal abundance was significantly greater in control compared to crab-tile plots at 12 h (ANOVA: $F_{1,32} = 17.85$, $p = 0.006$) but differences between treatments were not significant at 36 ($F_{1,32} = 0.05$, $p = 0.835$) and 144 h ($F_{1,32} = 0.79$, $p = 0.408$).

4172 individuals distributed among 43 nematode taxa were identified (Table 1). 15 taxa (35 %) were significantly overdispersed, indicating clumped spatio-temporal distributions (variance:mean ratio > 1 , $p < 0.05$), and were therefore downweighted in multivariate analyses (Table 1). *Terschellingia communis* and *Terschellingia longicaudata* were the most abundant species, together comprising 47 % of individuals per sample on average. The next most abundant species were *Ptycholaimellus ponticus* (15 %), *Axonolaimus paraspinosus* (7 %) and *Sabatieria pulchra* (6 %). Numbers of nematode individuals (N) and species (S) were significantly lower in crab-tile plots compared to control plots at 12 h (ANOVA, N: $F_{1,32} = 9.69$, $p = 0.021$; S: $F_{1,32} = 13.9$, $p = 0.01$). At 36 and 144 h, differences between treatments were not significant.

Nematode assemblage composition in the crab-tiled plots at 12 h differed from that in the control plots (ANOSIM $R = 0.594$, $p = 0.029$, Fig. 2). Differences in nematode assemblages between treatments had disappeared at 36 and 144 h ($R = -0.083$, $p = 0.771$; $R = 0.302$, $p = 0.114$). Differences between times within crab-tiled plots were, as expected, significant ($R = 0.641$, $p = 0.001$), reflecting differences between samples from 12 h and those collected at 36 and 144 h. Samples collected at 36 and 144 h did not differ significantly, however ($R = 0.26$, $p = 0.089$). Less expectedly, control samples also varied significantly through time ($R = 0.571$, $p = 0.001$), again reflecting differences between samples collected at 12 h and those collected at 36 and 144 h, which did not differ from each other ($R = 0.24$, $p = 0.171$).

Species contributing to differences between treatments at 12 h were all less abundant in, or absent from, crab-tiled plots (Table 1). The suites of species contributing to differences between control plots from 12 and 36 h, and crab-tiled plots from 12 and 36 h, were all similar and generally comprised the more abundant species on the mudflat.

4. Discussion

Resilience of an ecosystem can be defined as “the degree, manner and pace of restoration of initial structure and function after disturbance” (Westman, 1978). The most easily defined characteristic of ecosystem resilience is the rate of restoration (Sherman and Coull, 1980). Within 12-36 h of crab-tiling activities ending, significantly lower nematode abundance and species numbers had recovered to control levels. Multivariate analysis showed nematode assemblage composition in crab-tile plots to be comparable to controls after 36 h. The sampled intertidal mudflat meiofaunal communities can, therefore, be defined as resilient. This is supported by previous studies, which found meiofaunal recovery times from physical disturbance to vary between 12-48 h, depending on habitat type (Sherman and Coull, 1980; Hockin, 1982; Mistri et al., 2004).

The intermediate disturbance hypothesis links recovery rates to prevalent background disturbance regimes and habitat stability (Connell, 1978). Communities frequently exposed to physical perturbations tend to recover more quickly as they are dominated by species adapted to life in a dynamic environment (Gorzalany and Nelson, 1987). Marine assemblages in subtidal sands recover from physical disturbance more quickly than those in subtidal muds; the natural background

disturbance regime in the former is more energetic, so communities have adapted to high levels of natural disturbance (Kaiser, 1998; Collie et al., 2000). Microcosm studies indicate that nematode assemblages from sandy sediments are more resilient to physical perturbations than those from muddy sediments (Schratzberger and Warwick, 1998). However, unlike subtidal muds, intertidal mudflats are exposed to frequent natural disturbance, through tidal forces and currents, and the habitat is structured by these recurrent physical perturbations. Therefore mudflat communities, exposed naturally to repeat disturbances, may be expected to recover rapidly.

Abiotic factors indicate that crab tiling induced no significant changes to habitat structure. Recovery times can be longer when habitat characteristics are modified, and may take as long as 168 h when altered sediment characteristics persist (Cross and Curran, 2004). In these circumstances, some level of habitat recovery may be required before communities can recover (Dernie et al., 2003a; 2003b).

Due to the small-scale disturbance imposed by crab-tiling activity, it is probable that at least some recolonisation occurred via passive transport from densely populated adjacent sediment. Local dispersal is an important factor aiding persistence of populations following small-scale physical disturbance (Hiebeler, 2000) and recovery rate is related to the degree of community isolation (Chandler and Fleeger, 1983; Smith and Brumsickle, 1989). Nematodes and copepods are both passively resuspended and transported by tidal forces and currents (Sherman and Coull, 1980), and water-column meiofauna form a dispersing colonist pool that appears commonly in estuaries (Palmer, 1988) and allows rapid recolonisation of sediments (Sun and Fleeger, 1994). Meiofauna populations in muddy habitats are predominately located in the upper sediments and may have increased rates of dispersal, particularly as intertidal populations are regularly resuspended by tidal forces (Steyaert et al., 2003).

However, resuspension does not affect all taxa to the same degree; tidal currents particularly affect the small-scale distribution of harpacticoid copepods and to a lesser extent that of nematodes (Bell and Sherman, 1980).

It has been hypothesised that meiofauna that live close to the sediment surface are more susceptible to erosion and transport than deep dwelling species, so epigrowth-feeders may be expected to have relatively high dispersal rates, and populations may recover more rapidly following disturbance (Warwick and Gee, 1984).

Ptycholaimellus ponticus was a dominant species in both control and crab-tile plots, and has previously been found to quickly recolonise organically enriched sediment (Schratzberger et al., 2004a). That being said, the observed response to crab-tiling was a decreased abundance and range of species with differing feeding modes and ecological strategies, suggesting that whatever the direct effect of crab-tiling was, it had no species-specific component. The fact that control plots also had reduced abundances which recovered within 36 h suggests that the applied treatment had more widespread effects than expected, and therefore the mechanism by which crab-tiling disturbance reduces abundances cannot simply be via direct mortality.

Many meiofaunal taxa vertically migrate through sediments (Fay and Thistle, 1991; Palmer et al., 1992; Schratzberger et al., 2000) and vibrations through sediments may cause nematodes to bury deeper (Schratzberger et al., 2004a). Trampling of the sediment may have induced nematode populations to sink below the level of sampling, and this may be the reason for the apparent impact of, and recovery from, disturbance in the control plots. If disturbance intensity determined the depth of burial and number of nematodes that bury, then populations may have buried deeper in crab-tile plots where trampling occurred overhead, but also buried to a lesser extent in nearby controls. If nematode recolonisation of small-scale

defaunations is predominately via the same infaunal migration (Chandler and Fleeger, 1983; Schratzberger et al., 2004b), this would explain the rapid restoration of populations and may explain why community effects were not species specific. Taking deeper cores and vertical profiles of meiofauna communities would provide a better understanding of the mechanisms of impact and recovery by separating vertical migration and passive tidal transport in future studies.

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Table 1. Total abundance (N) of species in all samples, and average variance:mean ratio (D). * = Significantly overdispersed species ($D > 1$, $P < 0.05$ in an exact permutation test). SIMPER results: average raw abundances of species contributing up to a cumulative 90 % of dissimilarities between crab-tiled (T) and control (C) samples at 12 h, crab-tiled samples at 12 and 36 h, and control samples at 12 and 36 h. >, < denote species contributing more than 5 % of dissimilarity between groups. For the analysis overdispersed species (*) were downweighted by the value of D.

Species	N	D	T36	T12	C12	C36
%			90	80	59	
<i>Terschellingia longicaudata</i>	1041	13.1 *	58.5 >	4.2 <	18.5	46.0
<i>Terschellingia communis</i>	1037	7.3 *	61.0 >	3.5 <	18.7	43.3
<i>Ptycholaimellus ponticus</i>	483	2.5 *	32.7 >	2.0 <	7.0	27.3
<i>Sabatieria pulchra</i>	258	4.3 *	14.0	1.0	4.3	14.3
<i>Axonolaimus paraspinosus</i>	227	3.0 *	14.7 >	1.0	2.5	11.0
<i>Chromadora</i> sp.	124	2.9 *	6.3	0.5	4.5	4.0
<i>Atrochromadora</i> sp.	106	1.0	6.1 >	0.2	2.2	7.9
<i>Metachromadora</i> sp.	91	2.8 *	5.8	0.5	1.8	4.7
<i>Desmolaimus zeelandicus</i>	89	3.3 *	4.2	0.0	1.3	5.5
<i>Daptonema setosum</i>	88	2.1 *	5.0	0.2	1.2	9.2
<i>Daptonema oxycerca</i>	87	1.6 *	2.5	0.0	1.0	2.2
<i>Aponema torosa</i>	79	1.5	4.3	0.0	4.3	9.3
<i>Tripylloides gracilis</i>	69	1.5	5.6 >	0.4	1.9	3.7
<i>Chromadorita tentabunda</i>	53	1.9 *	2.8	0.0	0.5	4.7
<i>Oxystomina elongata</i>	50	1.8 *			0.3	2.5
<i>Leptolaimus papilliger</i>	44	1.2	2.9	0.3	0.6	
<i>Daptonema normanicum</i>	40	1.1	2.2	0.3	0.0	3.9
<i>Halalaimus</i> sp.	39	1.6	2.8	0.0	0.8	2.0
<i>Daptonema</i> sp.	29	1.3	3.0	0.3	1.3	4.0
<i>Theristus</i> sp.	23	1.5			0.0	1.5
<i>Molgolaimus demani</i>	21	2.2 *				
<i>Sabatieria celtica</i>	16	2.9 *				
<i>Spirinia</i> sp.	14	1.2				
<i>Microlaimus</i> sp.	12	1.0		0.0	0.5	
<i>Paralinhomoeus</i> sp.	9	1.0				
<i>Nudora bipapillata</i>	7	0.8				
<i>Viscosia viscosa</i>	7	1.0				
<i>Sphaerolaimus</i> sp.	5	0.8				
<i>Anoplostoma viviparum</i>	4	2.0 *		0.0	0.8	
<i>Eleutherolaimus stenosoma</i>	3	1.0				
<i>Linhomoeus</i> sp.	3	1.5				
<i>Dichromadora</i> sp.	2	1.0				
<i>Oncholaimus</i> sp.	2	0.7				
<i>Antomicron elegans</i>	1	1.0				
<i>Axonolaimus spinosus</i>	1	1.0				
<i>Campylaimus</i> sp.	1	1.0				
<i>Cyartoneura</i> sp.	1	1.0				
<i>Onyx</i> sp.	1	1.0				
<i>Paracanthonus</i> sp.	1	1.0				
<i>Praeacanthonus</i> sp.	1	1.0				
<i>Quadricoma scania</i>	1	1.0				
<i>Rhabditis marina</i>	1	1.0				
<i>Spilophorella paradoxa</i>	1	1.0				

Figure captions

Figure 1. Location (arrowed) of the crab-tiling experiment near the mouth of the River Yealm in Devon, UK.

Figure 2. Ordination by MDS of adjusted Bray-Curtis similarities calculated from dispersion-weighted nematode abundances in control (filled symbols) and crab-tiled (open symbols) plots at 12 ($\triangle$), 36 ($\circ$) and 144 (∇) h. Stress = 0.05.

Figure 1

Figure 2