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Parasites boost biodiversity and change animal community structure by trait-mediated indirect effects

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Parasitism has long been emphasised as an important process structuring animal communities. However, empirical evidence documenting the impact of parasites in other than simple laboratory settings is lacking. Here we examine the trait-mediated indirect effects of echinostome trematodes on a New Zealand soft bottom intertidal community of macroinvertebrates. *Curtuteria australis* and a second related but undescribed trematode both utilise the cockle *Austrovenus stutchburyi* as second intermediate host in which the parasites infect the foot tissue. Heavily infected cockles are therefore more sessile than lightly infected individuals, and, unable to bury, often rest on the sediment surface. We utilised these behavioural changes in two long term field experiments, respectively manipulating the parasite load of buried cockle (i.e. bioturbation), and the density of surfaced cockles (i.e. surface structures and seabed hydrodynamics). Both high parasite loads in buried cockles and the presence of surfaced cockles increased species richness and generally also the density of certain species and of major systematic and functional groups of benthic macroinvertebrates. Species diversity (alpha) peaked under intermediate densities of surfaced cockles. Our results demonstrate that parasites, solely through their impact on the behaviour of a single community member, can be significant determinants of animal community structure and function.

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Understanding the mechanisms that maintain biodiversity and structure natural communities is a central theme in ecological research. Among biotic processes recognised as especially important are competition and predation, but increasingly also parasitism (Minchella and Scott 1991, Begon et al. 1996, Hudson and Greenman 1998, Lawton 2000, Combes 2001, Shurin and Allen 2001). The evidence in support of the latter, however, rests largely on laboratory experiments on two-species systems and their mutual parasites, extrapolated to in situ community level. Here we describe a field experiment showing that a single type of parasite has profound community-wide effects in a New Zealand intertidal soft bottom assemblage of macroinvertebrates. This occurs solely through the parasites' impact on the behaviour of a bivalve community member, i.e. via trait-mediated indirect effects (Werner and Peacor 2003) as opposed to the traditionally emphasised density-mediated effects.

Trematode parasites are widespread in intertidal ecosystems where their complex life cycle usually includes several members of the animal community (Mouritsen and Poulin 2002). In addition to their potential for causing parasite intensity-dependent host mortality, parasites relying on trophic transmission often induce host behavioural changes in order to maximise transmission rates (parasitic manipulation, Mouritsen and Poulin 2002). The change of behaviour in such cases

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can be quite significant, and if a numerically dominant or in other way keystone species is involved, the manipulation process is likely to impact the surrounding animal community (Jones et al. 1997). To test this hypothesis, we selected the intertidal New Zealand cockle–echinostome association as a study system. We chose this system because it includes a host species that is dominant in the community in terms of both biomass and impact on sympatric invertebrate populations (Whitlatch et al. 1997), and involves well documented parasitic manipulation (Thomas and Poulin 1998, Mouritsen 2002).

Two species of echinostomes (Trematoda) are known to infect cockles (*Austrovenus stutchburyi*), both using an intertidal gastropod as first intermediate host, cockles as second intermediate hosts, and shorebirds as definitive hosts, the latter reached by trophic transmission. The two species, *Curtuteria australis* and a closely related but as yet undescribed species, are roughly equally abundant and ecologically equivalent in other respects (Allison 1979, Babirat et al. 2004). The parasites infect predominantly the foot tissue of the cockles, which interferes significantly with the bivalve's ability to move and rebury if dislodged to the sediment surface (Thomas and Poulin 1998, Mouritsen 2002, 2004). Consequently, heavily infected cockles are more sessile than lightly infected specimens, and the density of cockles found on the sediment surface of intertidal flats is strongly and positively related to the mean parasite load in the population as a whole (Mouritsen and Poulin 2003). We utilised these behavioural changes in two long term field experiments aiming at elucidating their impact on the benthic community. In the first experiment, we manipulated the mean parasite load of buried experimental cockles, altering their bioturbation potential. In the second experiment, we manipulated the density of cockles on the sediment surface, altering their impact on near-seabed hydrodynamics and sedimentary conditions.

Material and methods

Study site and experimental procedure

Experiments were carried out during the austral summer (November 2001 to May 2002) on the lower intertidal level (2 h exposure) of Gills Corner sand flat, Otago Harbour, South Island, New Zealand (45°50′S, 170°40′E). Here the infection intensity by echinostomes in local bivalves is relatively low and surfaced cockles are rarely found. We carried out two experiments simultaneously using a randomised block design in both: treatments were randomised within seven blocks distributed evenly along a 56 m transect parallel to the waterline. The two resulting experimental areas were separated by approximately five meter along the tidal gradient.

In one experiment (bioturbation experiment) we manipulated the mean parasite load of experimental cockles in the substrate and hence their bioturbation potential. The experimental unit was a 0.25 × 0.25 m frame (side height: 1 cm) pushed down just below the sediment surface, effectively separating the enclosed cockles from the surrounding population but allowing a roughly free exchange of other benthic organisms. Two treatments were assigned to each block: resident adult cockles were removed from the frames one by one by hand and replaced by 100 similar-sized adult cockles from either Otakou (low parasite load) or Company Bay (high parasite load), also in Otago Harbour. The density of experimental cockles (400 m^{-2}) corresponded approximately to the natural adult density (around 420 m^{-2}). Measurements and dissections of a subset of experimental cockles demonstrated similar average (±SE) shell length (Otakou: 30.9 ± 0.3 mm; Company Bay: 30.6 ± 0.3 mm; student's t-test, $t_{60} = 0.81$, $p = 0.42$) and significantly different mean parasite load (Table 1). At the end of the experiment (six month duration), we took two 15 cm deep core samples (each 0.012 m^2) from each treatment plot and sieved them together on a 500 μm screen. All animals retained were preserved in 4% formaldehyde, and under a dissection microscope enumerated and identified to the lowest taxonomical level possible. Cockles remaining in each treatment plot after the experiment were counted as well. To evaluate the two types of experimental cockles' crawling activity as a measure of their bioturbation potential, we performed a 4 day mark–recapture experiment. Fifteen similar-sized cockles from both Otakou and Company Bay were individually marked and placed at their natural burying depth in the sediment, and the linear distance from the point of release to the site of recapture was measured.

In the second experiment (surfacing experiment) we manipulated the density of experimental cockles on the sediment surface and hence their impact on near-seabed hydrodynamics and sedimentary conditions (Nowell and Church 1979, Soulsby 1997). The experimental unit was a 1 × 1 m plot crossed by 10 parallel fishing lines attached to peripheral lines anchored into the sediment by pegs. Three treatments with none, 30 and 100 cockles attached, respectively, were established. At sites of heavy infections, the natural densities of surfaced cockles may exceed 50 m^{-2}, and thus the experimental densities we used cover the gamut of possibilities. The experimental cockles were cockleshells glued shut (with clay enclosed to obtain approx. natural buoyancy) and attached to 6 cm fishing lines that in turn were attached to the parallel fishing lines in a random pattern. The cornerpegs were hammered down below the sediment surface and the parallel fishing lines were gently pushed

Table 1. Bioturbation experiment: effect of low and high cockle parasite load on cockle mobility and resulting macrofaunal density and diversity. Values are means (SE) and $n = 7$ per treatment if not otherwise stated. Low and high parasite loads were 33.0 ± 3.1 (SE) and 426.2 ± 37.5 echinostome metacercariae cockle^{-1}, respectively ($n = 31$, student's t-test, $p < 0.0005$). Experimental cockles have been excluded in calculation of diversity indices; $2^{H'}$ is sensitive to the abundance of the rare species whereas D^{-1} is more sensitive to common species, and values denote the number of evenly common species required to obtain the H'-value observed in the sample. Simpson's evenness index measures the relative abundance of species, and ranges between 0 and 1 (all evenly abundant). P = polychaete, B = bivalve, H' = Shannon–Wiener index, D = Simpson's diversity index, s = number of species in sample.

Parameter	Cockle parasite load		p†
	Low	High	
Cockle mobility			
proportion relocating (%)	93.3	20.0	<0.001‡
mean distance moved (cm)§	22.4 (3.9)	4.0 (1.5)	0.001¶
Density (individuals 0.024 m^{-2})			
species affected			
Capitellidae sp. 2 (P)	0.3 (0.2)	1.3 (0.4)	0.018
Exogone heterosetosa (P)	32.0 (4.0)	49.7 (6.4)	0.043
Nucula dunedinensis (B)	3.0 (0.6)	5.9 (1.1)	0.035
Gastropoda combined	0.9 (0.4)	2.7 (0.7)	0.026
rare species combined††	3.9 (0.7)	7.4 (1.4)	0.027
total fauna	107.6 (9.1)	140.9 (11.6)	0.044
Species richness (no. species)			
mean no. sample^{-1} (0.024 m^2)	18.3 (0.2)	20.3 (0.8)	0.026
total (0.168 m^2)	34	36	
Species diversity indices			
Shannon–Wiener ($2^{H'}$) (species)	6.95 (0.76)	6.94 (0.99)	0.99
Simpson's (D^{-1}) (species)	6.39 (0.48)	5.36 (0.29)	0.043
Simpson's evenness index (1/Ds)	0.35 (0.03)	0.27 (0.02)	0.005

†Paired t-test or Wilcoxon paired signed ranks test if not otherwise stated.
‡Fisher's exact test.
§Based on relocating individuals only; $n = 14$ and $n = 3$ for low and high parasite load, respectively.
¶Student's t-test.
††Species with less than one individual sample^{-1} on average.

into the substrate. This left no other part of the experimental setup but the cockles (if present) on the surface. The use of anchored cockles was necessary to maintain the experimental densities of surfaced cockles throughout the duration of the experiment. Mean length ($\pm$SE) of experimental cockles was 31.2 ± 0.3 mm ($n = 50$). After six months, we took five core samples (each 0.012 m^2) in each treatment plot that were processed as for the bioturbation experiment, except that each sample was treated separately. When experimental cockles were included in a sample, all attached animals were rinsed into the sieve together with the rest of the sample. Animals present on remaining surface structures (experimental cockles, various shells, etc.) within each experimental plot were collected in a similar way in order to separate epifaunal and infaunal organisms. Species in samples of attached animals were considered epifauna if they occurred in a density equal to or greater than their density in core samples. In addition, five 5 cm deep sediment cores (diameter = 4 cm) were collected in each plot for analysis of particle composition, carried out on a Rapid Sediment Analyser using a settling tube and in association with MacRSA version 2.0.6 software (Ballard 1990). Furthermore, visual inspection of treatment plot prior to sampling revealed that in contrast to control and 30-cockle plots, 100-cockle plots had an elevated seabed in comparison to the surrounding sand flat. In order to quantify this, two 100-cockle plots were levelled by measuring the distance between the sediment surface and a level fixed above the substrate at seven positions inside and six positions outside each plot.

Data analysis

Information on the general mode of life of the animals collected was extracted from a range of local handbooks, electronic library databases and, regarding feeding mode, also from the dissection of specimens. Calculation of the various indices followed Krebs (1999). Both Shannon–Wiener and Simpson's species diversity index was expressed in units of species (measured as $2^{H'}$ and D^{-1}, respectively), which denote the number of evenly abundant species required to generate the observed heterogeneity of the sample. Whereas H' emphasises rare species, D emphasises common species (Krebs 1999). Sediment particle size is expressed in phi-values (Φ) and the sorting coefficient represents the number of Φ-units occurring between the first and third quartile diameter (Buchanan 1984). Statistical analyses were carried out in SPSS 10.0 (SPSS 1999). Parametric tests were preceded by tests of their assumptions, and if the latter were violated, data were transformed or nonparametric statistics were applied. Two-way ANOVAs was carried out on un-, ln- or rank-transformed data from the surfacing experiment (Table 2, Fig. 1, 2), evaluating the effects of treatment, block and their interaction. In a few cases, a highly significant treatment effect was accompanied by less significant block effect or interaction. In any event, only the p-value of the treatment effect is given in Table 2. In cases where the error-variance of the two-way ANOVA could not be stabilised by transformations, a chi-square based Kruskal–Wallis test was performed to evaluate treatment effects.

Results

The bioturbation experiment

The mark–recapture experiment confirmed that high parasite loads significantly reduce the cockles' ability to move (Table 1), which means that the disturbance of the upper sediment strata is substantially relaxed in plots with heavily infected cockles. Consequently, the structure of the benthic animal community changed (Table 1). The density of three species increased significantly, including the community's most abundant species; all three are very small and therefore particularly sensitive to disturbance of the upper sediment strata. In addition, gastropods as a major taxonomical group increased in density (four species), as did rare species combined (11 species). In effect, the total abundance of all macroinvertebrates increased by more than 30%, suggesting elevated zoobenthic biomass where infection levels of cockles are high. Species richness was higher in the high than in the low parasite load treatments, both on average and in total (Table 1). By contrast, the species diversity (alpha) remained unaffected (Shannon–Wiener index, emphasising rare species) or reached its minimum in the treatment with the highest cockle parasite load (Simpson's index, emphasising common species). The difference between the two diversity indices results from the increased density of a few common species in the high parasite load treatment, in line with a significantly less even relative abundance of species in that treatment (Simpson's evenness index, Table 1).

Because the density of cockles that remained after the experiment was similar between treatments (on average 90 individuals in both; student's t-test, $t_{12} = 0.14$,

Table 2. Surfacing experiment: effect of different densities of surfaced cockles on macrofaunal densities, species richness and sediment properties. Treatment: number of experimental cockles m^{-2} on surface. Values are means (SE) and n = 35 per treatment if not otherwise stated. N = nemertine, Pr = predator, P = polychaete, D = deposit feeder, C = crustacean, SD = selective detritus feeder, G = gastropod. Gr = grazer.

Parameter	Treatment			p†
	0	30	100	
Density (individuals 0.012 m^{-2})				
species affected				
Nermertea sp. 1 (N, Pr)	0.03 (0.03)	0.06 (0.04)	0.31 (0.11)	0.012
Capitellidae sp. 2 (P, D)	5.2 (1.4)	6.3 (0.8)	2.9 (0.5)	0.003
Heteromastus filiformis (P, D)	10.2 (0.7)	13.1 (0.8)	12.9 (0.7)	0.009
Exogone heterosetosa (P, D)	46.7 (3.0)	48.5 (2.7)	56.9 (2.5)	0.004
Exogone sp. 2 (P, D)	1.1 (0.2)	2.0 (0.4)	0.9 (0.2)	0.005
Lysianassidae sp. 1 (C, SD)	0.03 (0.03)	0.26 (0.10)	0.40 (0.10)	0.004
Notoacmea helmsi (G, Gr)	0.14 (0.06)	0.54 (0.19)	1.14 (0.20)	<0.001
Micrelenchus huttonii (G, Gr)	0.03 (0.03)	0.49 (0.13)	0.60 (0.18)	0.001
Diloma subrostrata (G, Gr)	0.06 (0.04)	0.29 (0.10)	0.60 (0.19)	0.011
epifauna	1.5 (0.2)	2.9 (0.4)	4.5 (0.6)	<0.001
infauna	119.4 (5.4)	137.5 (5.4)	137.5 (5.0)	0.005
total fauna	120.9 (5.5)	140.4 (5.4)	142.0 (5.1)	0.009
trophic groups				
predators	6.7 (0.9)	8.1 (1.1)	8.2 (0.8)	0.27
deposit feeders	92.6 (4.3)	104.3 (4.1)	107.1 (3.9)	0.009
selective detritus feeders	13.7 (1.8)	19.0 (2.3)	15.9 (1.4)	0.022
grazers	0.2 (0.1)	1.3 (0.3)	2.4 (0.4)	<0.001
filter feeders	7.6 (0.4)	7.7 (0.5)	8.4 (0.5)	0.31
Species richness (no. species)				
treatment level‡	32.1 (1.0)	36.6 (1.0)	37.1 (1.2)	0.008
total§	56	62	65	
Sediment properties				
particle diameter (Φ)¶	2.18 (0.01)	2.22 (0.01)	2.17 (0.01)	0.001
sorting coefficient (Φ)¶	0.29 (0.00)	0.31 (0.01)	0.29 (0.01)	0.017
finer particles (<150 µm) (%)	4.4 (0.3)	6.6 (0.5)	4.7 (0.5)	0.003

†Two-way ANOVA or Kruskal–Wallis test (Material and methods).

‡Core samples within treatment plots combined (0.06 m^2) (n = 7).

§All species recorded from core samples and epifauna samples combined.

¶In Φ-units, which equal –ln(particle diameter in mm)/ln2; a high sorting coefficient means a highly diverse sediment regarding particle composition.

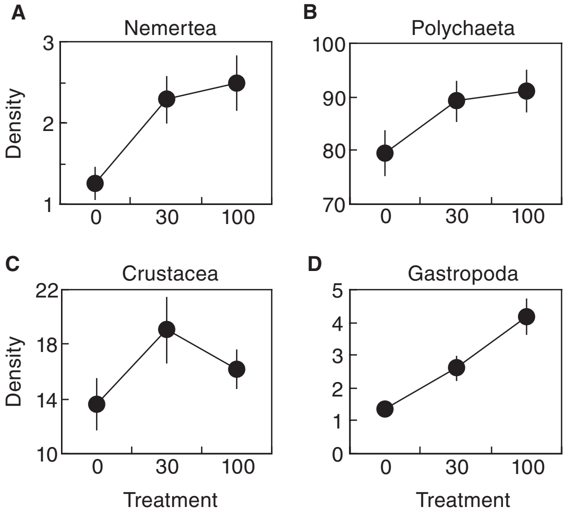

Fig. 1. Density of major taxonomical groups of animals (No. individuals sample^{-1}) as a function of the number of cockles on the sediment surface. Values are means ($\pm$SE), $n = 35$. Treatment: number of experimental cockles m^{-2} on surface. (A) Nemertea, including 4–6 species (depending on treatment). (B) Polychaeta, including 20–25 species. (C) Crustacea, including 12–16 species. (D), Gastropoda, including 5–6 species. All groups are significantly affected by treatment (Nemertea: $p = 0.005$; Polychaeta: $p = 0.038$; Crustacea: $p = 0.032$; Gastropoda: $p < 0.0005$).

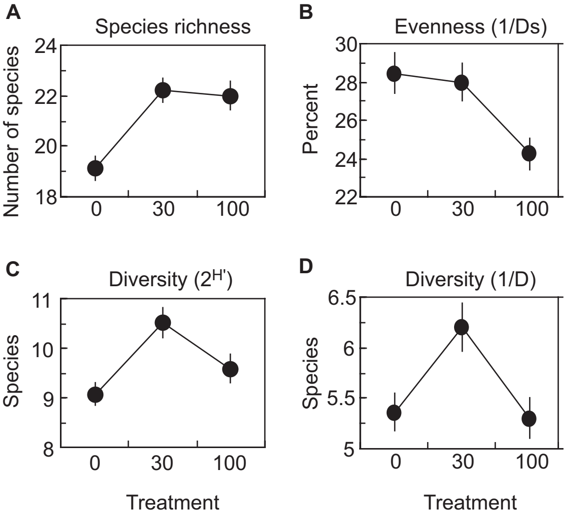

Fig. 2. Macrofaunal diversity as a function of the number of cockles on the sediment surface. Values are means ($\pm$SE), $n = 35$. Treatment: number of experimental cockles m^{-2} on surface. (A) Species richness (number of species sample^{-1}). (B) Simpson's measure of evenness, here expressed in percent. (C) Shannon–Wiener diversity index with emphasis on rare species. (D) Simpson's diversity index with emphasis on common species. See Table 1 for abbreviations and further indices account. All measures are significantly affected by treatment (species richness: $p < 0.0005$; evenness: $p = 0.002$; $2^{H'}$: $p = 0.004$; 1/D: $p = 0.005$).

$p = 0.89$), with none found on the sediment surface, the differences in the benthic animal community between treatments can be attributed solely to the parasite-induced difference in bioturbation by cockles.

The surfacing experiment

The presence of cockles on the sediment surface had an even more profound impact on the structure of the benthic community than parasite-induced relaxed bioturbation. The density of nine species, together representing a wide range of taxa, feeding types and relative abundance, changed significantly (Table 2); seven of the nine species increased in density with increasing density of surfaced cockles, but one (*Exogone* sp. 2) clearly favoured intermediate conditions, and one (Capitellidae sp. 2) was negatively affected by high numbers of surfaced cockles. In total, the density of macrobenthic animals was significantly higher in treatments with surfaced cockles than in controls (Table 2). Focusing on major taxonomic groups, the density of nermertines, polychaetes and gastropods increased with increasing number of surfaced cockles, whereas the abundance of crustaceans peaked at intermediate numbers (Fig. 1). Bivalves (six species), on the other hand, were unaffected by the treatments ($p > 0.15$). Thus, the overall taxonomical composition of the benthic community changed as a function of experimental treatment, that is, as a function of the mean infection intensity in the cockle population.

Overall community function also appears significantly influenced by cockle parasitism. Whereas the density of predators and filter feeders remained unchanged, the abundance of deposit feeders and grazers increased with increasing density of cockles on the surface, and selective detritus feeders were most numerous at a moderate density of surfaced cockles (Table 2). Although predators were numerically unaffected, the species composition of the predator-guild changed. The density of predatory polychaetes decreased as a function of increasing number of surfaced cockles, while other predators (e.g. whelks, nemertines) increased in abundance (two-way interaction, $p = 0.006$). A similar two-way interaction was evident between the density of tube-dwelling and free-living species ($p = 0.0025$), peaking at intermediate and high densities of surfaced cockles, respectively. The presence of animal tubes in soft bottom habitats can severely affect the stability of the substrate, in turn influencing the living conditions of other benthic organisms (Eckman et al. 1981, Rhoads and Boyer 1982). In contrast, there was no significant treatment-dependent interaction between the abundance of epi- and infaunal organisms ($p = 0.29$), and both groups of animals were positively affected by the presence of surfaced cockles (Table 2).

In addition to the community's numerical response, species richness, species diversity (alpha), and evenness were also significantly influenced by the presence of surfaced cockles. The mean number of species sample^{-1} was significantly higher in treatments with cockles on the surface (Fig. 2A), and at the larger spatial levels (experimental plot and treatment levels) the species richness tended to peak in plots with most cockles on the surface (Table 2). The relative abundance of species was, however, most heterogeneous in the 100-cockle treatment (low evenness index, Fig. 2B), which in part accounts for the fact that the species diversity reached its maximum at the intermediate number of surfaced cockles (Fig. 2C, D).

The treatment-induced changes in the benthic animal community were accompanied by significant changes also in sediment characteristics and the rate of sedimentation. The mean particle diameter, sorting coefficient (i.e. particle size diversity), and the proportion of finer particles all peaked in the presence of an intermediate density of surfaced cockles (Table 2). In contrast to the control and 30-cockle plots, all 100-cockle plots had elevated seabed. Levelling of two such plots confirmed a significant elevation of respectively 52 and 73 mm relative to the surrounding flat (student's t-test, $t_{11} > 3.09$, $p \leq 0.01$).

Discussion

The results from the bioturbation and surfacing experiments together demonstrate that parasites can be potent determinants of the structure and function of soft bottom animal communities solely through trait-mediated indirect effects (Werner and Peacor 2003). Such a role has hitherto been exclusively attributed to predation and competition in soft bottom ecosystems (Wilson 1991). In other systems where parasites have been recognised as potentially important, their impact is generally assumed to be mediated by changes in host density, i.e. parasites affect the abundance rather than the phenotype of a keystone predator or competitor (Hudson and Greenman 1998, Combes 2001). Our study also provides an example of how a parasite can completely alter the potential of its host to act as an ecosystem engineer (Jones et al. 1997).

Whereas parasite-induced relaxed disturbance of the sediments can readily be identified as the mechanism behind the community changes observed in the bioturbation experiment, the picture is more complex in the case of the surfacing experiment. Here, the treatment-dependent structural and functional changes of the benthic community are likely generated by a combination of two very different processes, respectively affecting the epi- and infauna. Epifaunal organisms may benefit directly from the presence of more surface structures used either as substrate for attachment or feeding, or as shelter under which they can hide during low tide. The infauna, on the other hand, is most probably affected indirectly through the surfaced cockles' modification of the hydrodynamics at the substrate–water interface, which in turn influences the particle composition in the upper sediment strata. Sediment properties are important distributional factors for infaunal organisms (Snelgrove and Butman 1994), and they clearly differed between treatments: the mean particle diameter, sorting coefficient, and the proportion of finer particles peaked at an intermediate density of surfaced cockles. Current induced erosion around surfaced cockles, in addition to deposition of fine particle in the cockles' lee side, may account for this (Soulsby 1997). In the 100-cockle treatment, however, the area occupied by surfaced cockles (about 8%) may have induced skimming-flow, which significantly mitigates the turbulence at the sediment–water interface and increases sedimentation (Nowell and Church 1979). In effect, the sediment properties of the 100-cockle treatment will correspond to those of the control, with an elevated seabed in comparison to the surrounding sand flat, as also observed.

Our results apply at the very least on a local scale (metres to tens of metres). On larger scales, however, the impact of the parasites may be reduced due to small scale vertical and horizontal variation in the level of parasitism and disturbance of the upper sediment strata, which together brings the cockles to the surface (Mouritsen et al. 2003, Mouritsen and Poulin 2003, Mouritsen 2004, unpubl.).

Besides providing evidence for a major role of parasitism in community ecology, our results also support the intermediate disturbance hypothesis (Connell 1978). Species diversity in the surfacing experiment peaked at intermediate infection intensities, supporting the intermediate disturbance hypothesis' predicting that diversity will be highest at intermediate levels of disturbance (Connell 1978, Petraitis et al. 1989). The peak in species diversity also coincided with the highest particle diversity in the substrate, suggesting that sediment diversity is an important distributional factor in infaunal communities of macroinvertebrates. This finding mirrors observations from deep-sea environments (Etter and Grassle 1992).

The host–parasite system studied here is by no means unique, and parallels can be found in soft bottom habitats in the northern hemisphere (Lauckner 1983). This indicates that the community-level effects of parasitism we observed are likely to be of widespread importance. There are innumerable host–parasite systems where either host behaviour or abundance is significantly affected, and our study is the first field experimental attempt to elucidate the community wide effects of just one of these systems. Unravelling the community-level impacts of parasitism may therefore be critical to a better understanding of why species assemblages and communities are structured in the way they are.

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