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Predator caging experiments: a test of the importance of scale

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Abstract

The impact of predators is often relative to the spatial scale at which the study is conducted. In this paper we investigated how spatial scale might influence the importance of predation. In doing this we addressed the hypothesis of scale-dependency in predation experiments. The predator studied was the shore crab, *Carcinus maenas* (L.), and its impact on intertidal macrofauna communities was assessed using a caging experiment. Two different treatments, small and large enclosure cages (of, respectively, 0.25 and 1 m^2), were established in a completely randomised design on two different sites, mud and muddy sand, which differed physically but were very similar biologically. The density of crabs per square metre was 48, much larger than the ambient density but comparable with previously published work. The experiment ran for a month and the resulting data and summary statistics were analysed using univariate and multivariate methods. Results indicate that the impacts of crab predation were similar in the different cage sizes but different on the different sites. The present work demonstrates the importance of scale in interpreting the results of caging experiments, but not at the small-scale level of cage size.

Keywords: Caging experiments; Cage size; Scale; Grain; Extent; Soft-sediments

1. Introduction

Two different types of constraint act to delimit the relevant domain of results from manipulative experiments. First, artefacts will always be created by the experimental

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procedure. These can be controlled for, and their impact on the phenomena of interest might be slight compared to the impact of the experimental variable. Nevertheless, doubt will always remain over the accordance of experimental results and real world, 'artefact-free' processes. Second, whilst experimental results might be reliable for one particular place, different conditions might prevail elsewhere. The spatial scales over which experimental results are relevant are often unknown. This paper considers both of these constraints in the context of a predator caging study in the soft-sediment intertidal.

Caging experiments have been widely used in marine ecology (Reise, 1985; Hall et al., 1990a). They are often the best or only means of investigating how particular species (usually predators) structure a community. The potential for artefacts in such experiments has been recognised for many years (Virnstein, 1978). Effects such as increased sedimentation within cages, the clogging of cages by weeds and debris, differences in cage shape, changed predator behaviour within cages, could all confound experimental results, and are discussed elsewhere (e.g. Hulberg and Oliver, 1980; Virnstein, 1980; Jumars and Nowell, 1984; Nowell and Jumars, 1984; Leber, 1985; Reise, 1985; Hall et al., 1990a).

One issue which has not been well addressed, however, is that of the appropriate size of cage. When sampling spatially patchy populations, the size of the sampling unit (such as a quadrat) is likely to have important implications for the results (see e.g. Southwood, 1978). The same issues are pertinent when considering cage size; the cage represents the maximum possible sample area per replicate. In reality, most experimenters sub-sample smaller areas within their cages. If the cage is smaller than the typical patch size of the organism or organisms of interest, many replicates will be needed to provide reliable results. Nevertheless, matching cage size to patch size might not resolve these issues since spatial patterns themselves are dependent on scale (Thrush et al., 1994).

Cage size could exert effects in many ways other than simply circumscribing sample area. For open predator caging experiments (those allowing the movement of prey into and out of cages), simulation (Hall et al., 1990a; Englund, 1997) and field (Englund and Olsson, 1996) studies have shown that the migration rates of prey can substantially affect results. Frid (1989) and Hall et al. (1990a) discuss the effects of prey movements on predator impact and suggest that, in certain cases, they might mask predator effects in small cage experiments. In addition, the effects of prey movement are scale dependent. The larger the cage, the less likely prey movements will confound predator effects. Thus Englund (1997) predicts that 'the results from open predation experiments should be highly scale dependent. It is quite conceivable that a small-scale manipulation will strongly affect one species but leave another one unaffected, whereas a larger scale manipulation produces the opposite result'.

Increasing cage size is also likely to increase the chance of finding indirect effects in a caging experiment, since larger cages are likely to contain more complex interactions than smaller ones. Indirect effects might result from predators changing the balance of competition, or preying on other predators in the cage, and could be important in structuring some systems (e.g. Kneib, 1988; Martin et al., 1989), so cages should be large enough to contain representative communities.

The arguments above suggest that caging experiments should always use the largest cages possible. However, limitations on resources, the possibility of disturbances (from

vandalism or physical forces such as wave action) and the need for replication work against this advice. It would normally therefore be very useful to know how large cages have to be in order to show genuine community and population level effects of predation. Experiments to answer this question would entail applying the same treatment to a range of cage sizes. To our knowledge, there are no field studies which do this. The first objective of the work described in this paper was to begin this task using two different sizes of cage. In doing this we aimed to test the Englund (1997) prediction of scale dependence in predation experiments. Our null hypothesis is that cage size will have no effect on the results of our experiment.

Thrush et al. (1997), and references therein, identify three components of scale, of which the cage or sample size – the *grain* – is the smallest. Their largest category, the *extent*, refers to the total area over which samples are collected (or experimental replicates distributed). The spatial relevance of an experiment's results will depend on the extent to which variability within the extent of the experiment represents variability found within the habitat as a whole. Many apparently homogenous environments, such as mudflats, can be very spatially heterogeneous at a range of scales (Morrissey et al., 1992), therefore, considerations of experimental design to deal with heterogeneity are of utmost importance (Dutilleul, 1993). Extrapolating from relatively small extent experiments to larger areas of habitat is a major problem in ecology (Thrush et al., 1997; Thrush, 1998). For example, some predators forage differently in different sediments, (Quammen, 1980; Lipcius and Hines, 1986; Sponaugle and Lawton, 1990; Eggleston et al., 1992). The results of a predator caging experiment in one area of a mudflat might therefore be misleading if applied to the mudflat as a whole, even if the prey species are the same over the whole habitat. The second objective of this work was to test the effects of running the same experiment in two adjacent areas known to differ physically (in their sediment characteristics) whilst being very similar biologically. Our null hypothesis is that there will be no significant differences in the experimental results recorded in the two sites.

2. Methods

2.1. Field site

The study was conducted on the intertidal mud flats immediately east of Blackness Castle, on the south side of the Forth estuary, eastern Scotland (56° 0′ N, 3° 30′ W). This flat consists of an area of approximately 1 km^2 of mud and muddy sands. Experimental blocks were located at mid-tidal level.

2.2. Experimental design and sampling

Two different treatments (small and large enclosure cages) were established on two different sites (mud and muddy sand). Cages consisted of four wooden corner posts, 0.5 m high, joined 0.1 m from the base with a 0.1-m wide strip of plywood, and covered

with 3 mm mesh plastic netting. Large cages enclosed an area of 1 m^2; small an area of 0.0625 m^2 (0.25×0.25 m).

At each site, 20 cages were placed in a 5×4 grid, with 3 m between each cage. Five replicates each of small enclosure and large enclosure treatments, and five replicates each of small and large controls, were randomly allocated within the grid. All cages were pushed 0.2 m into the sediment, burying the basal strip of plywood and leaving 0.3 m above the sediment. This design prevents crabs escaping from the enclosures by burrowing (Raffaelli et al., 1989). Forty eight crabs (*Carcinus maenas*, henceforth *Carcinus*) were enclosed in large treatment cages, 12 in small treatment cages, giving a crab density in both treatments of 48 per m^2. All crabs measured between 15–25 mm carapace width, and were captured immediately prior to enclosure at the experimental site. Crabs with soft carapaces and/or damaged chaela were not used. Routine sampling had shown that *Carcinus* of this size occur naturally at this site at densities of up five per m^2 (M. Richards, Napier University, unpublished data). They do not show tidal migration, but remain buried in the sediment at low tide (Hunter and Naylor, 1993). Control cages were identical to treatment cages but no crabs were enclosed.

The two sites are at the same tidal level, 50 m apart. Sediment at the muddy site (MS) is finer and contains more carbon than at the sandy site (SS); fraction < 63 μm, 0.29 MS, 0.1 SS; %carbon 6.4 MS, 2.8 SS.

The experiment was established on 3 September 1996. On 4 October 1996, all cages were searched for surviving crabs. Then 0.1×0.1 m cores for faunal analysis were taken, to a depth of 6–7 cm, from randomly chosen points within the cages; three cores were taken from large cages, and two from small to account for small-scale variability within cages. A single 3-cm diameter core, for sediment analysis, was taken from a randomly chosen position in each cage to a depth of 4 cm. All faunal cores were split into two layers. The top 1 cm was sieved over a 212-μm mesh, the remaining 5–6 cm over a 500-μm mesh, and all organisms retained were fixed in 10% formaldehyde with rose bengal dye, before being stored in 70% alcohol. Faunal cores were pooled and results averaged to give an overall result per cage.

All macrofauna (with the exception of nematodes) were counted and identified to species level, where possible. Sediment samples were analysed for carbon content by loss of weight on ignition at 460°C (Holme and McIntyre, 1984).

2.3. Data analyses

Treatment (crabs present or absent), site and cage size were treated as fixed factors in three-way model I ANOVA tests for differences between the mean abundances of the dominant taxa found. All data in these tests were first $\log_{10}(x + 1)$ transformed, and checked for normality and homoscedasticity.

Total abundance (of all species), number of species, Shannon–Wiener diversity ($\log_{10}$) and Margalef's M ($\log_{10}$) were calculated as summary univariate statistics for each treatment category. Data were $\log_{10}$ transformed where required, and three-way ANOVA used to test for differences. A total of 15 three-way ANOVA tests were performed. To reduce the chances of within-experiment type I error, a conservative

correction, the Bonferroni correction, was applied to alpha values, such that only values $\leq 0.05/15 = 0.003$ were considered significant.

Since some summary univariate statistics are sensitive to sample size (Magurran, 1991) further analyses on the impacts of crabs on prey were conducted. The mean number of all individuals and mean number of species in treatment and control cages (of both sizes) were calculated for both sites. In order to correct for any initial differences in absolute values of numbers of individuals and numbers of species in the two sites, the percentage change in both variables was calculated as: (controls mean − treatments mean)/controls mean. To test for significant differences between the values for the two sites, an estimate of the percentage change in these two variables was calculated for each treatment cage, at each site. Treatment cages were matched to their nearest control cage (regardless of size), and percentage change calculated as above. This provided ten individual values for each variable for each site. After arcsine transformation, *t*-tests (Minitab unpooled correction) were used to test for significant differences between the mean percentage change in species number and number of individuals in the two sites.

Multivariate data analyses, performed using the PRIMER (Plymouth Routines in Multivariate Ecological Research) package, were by hierarchical clustering using group-average linking with the Bray–Curtis similarity measure and non-metric multi-dimensional scaling ordination (MDS), followed by analyses of similarities (ANOSIM) to assess if there were any significant differences between the different treatments and controls (with global and pairwise differences assessed – Clarke and Warwick, 1994). Data were square root transformed for these analyses.

3. Results

Mean crab survivorships in the four different treatments were: large mud, 21; large sand, 30; small mud, 9; small sand, 9. One crab in the same size range as the experimentally added crabs was found in a large control cage. As numbers in controls and treatments did not, therefore, overlap, data from all plots were included in the analyses.

Two samples were accidentally lost, reducing replication in the small treatment cage group at the muddy site and small control cage group at the sandy site to four. An error during processing led to the pooling of sediment samples within cage and sediment types. It was therefore only possible to calculate % carbon values at the end of the experiment from these pooled samples: large cage, mud, 6%; small cage, mud, 6.8%; large cage, sand, 2.8%; small cage, sand, 2.8%.

A total of 28 taxa were recorded, all of which are included in the multivariate and summary univariate tests. The 11 most abundant taxa (taxa which occurred in all treatments, or in high numbers in one or more treatments, or both) were individually tested for differences in mean abundance between treatments.

3.1. Univariate tests

Untransformed summary univariate data satisfied the conditions for ANOVA with the

exceptions of abundance and Margalef's, which were transformed. Data for tests on mean abundance of individual taxa were all $\log_{10}$ transformed.

There is no evidence that cage size affected taxa abundance, diversity or richness (Fig. 1, Table 1), and no interaction effects were found between size and predation or site in any of the tests. Crab predation had a highly significant impact on abundance, number of species and Margalef's richness (Fig. 1, Table 1), and there were significant interactions between predation and site in the tests on abundance and Margalef's richness. There was significantly lower abundance and Margalef's richness on the sandy sediment site. Crabs caused significantly higher mean percentage reductions (one-tailed *t*-tests: number of individuals, $t = 3.81$, $df = 14$, $p = 0.0019$; number of species, $t = 1.84$, $df = 11$, $p = 0.046$) in the total number of individuals and number of species in the sandy site (total reduction of 89% individuals and 30% species) compared with the muddy site (total reduction of 69% of individuals and 8% species).

In the single species tests, only one significant interaction was found between predation and site (*Pygospio elegans*; Fig. 2, Table 2). Crab predation significantly reduced the abundances of the four mollusc species, *Hydrobia ulvae* (Pennant),

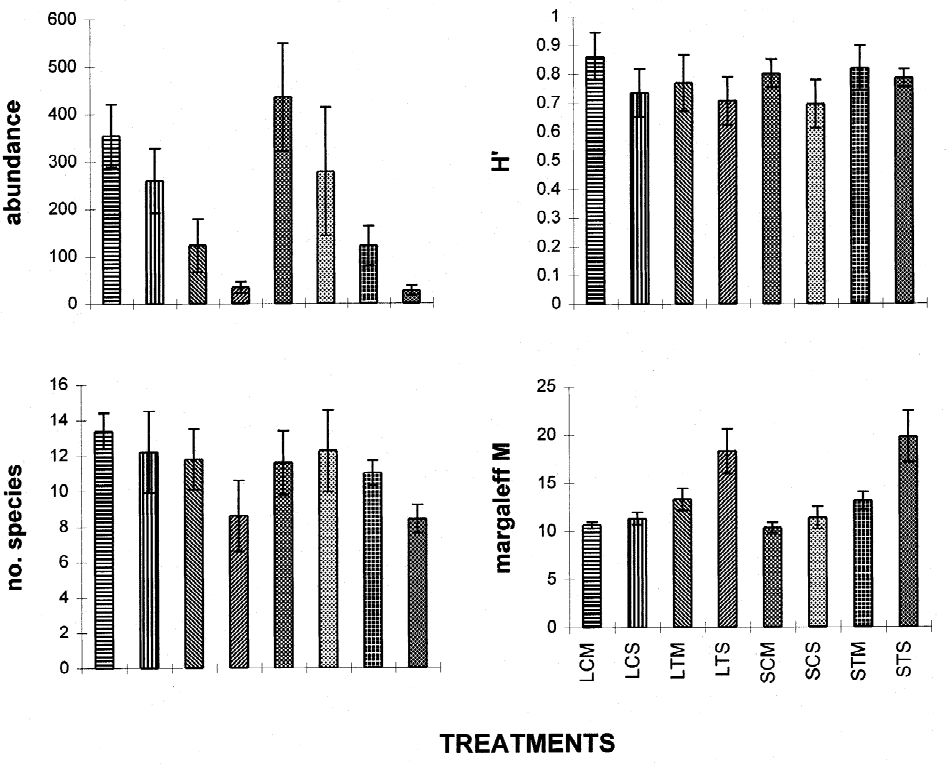

Fig. 1. Mean univariate measures of macrofaunal community structure in all combinations of cage size, site and treatment (crabs present or absent) with 95% confidence intervals. Legend key: LCM, large control mud; LCS, large control sand; LTM, large treatment mud; LTS, large treatment sand; SCM, small control mud; SCS, small control sand; STM, small treatment mud; STS, small treatment sand.

Table 1
Three-way analysis of variance, with interaction terms, of univariate summary statistics[a]

Source	df	MS	*F*	*P*
Log(10) abundance				
Treatment	1	5.18	159	**0.000**
Site	1	1.51	46.5	**0.000**
Size	1	0.00	0.00	0.977
Treatment × Site	1	0.43	13.5	**0.001**
Treatment × Size	1	0.01	0.53	0.473
Site × Size	1	0.02	0.75	0.394
Treatment × Site × Size	1	0.01	0.05	0.831
Residual	30	0.03		
No. taxa				
Treatment	1	54.7	15.3	**0.000**
Site	1	23.7	6.6	0.015
Size	1	4.45	1.25	0.273
Treatment × Site	1	16.2	4.54	0.041
Treatment × Size	1	0.33	0.09	0.763
Site × Size	1	3.53	0.99	0.328
Treatment × Site × Size	1	0.92	0.26	0.616
Residual	30	3.57		
Shannon–Wiener diversity				
Treatment	1	0.00	0.02	0.893
Site	1	0.06	9.08	0.005
Size	1	0.00	0.07	0.800
Treatment × Site	1	0.01	1.53	0.226
Treatment × Size	1	0.03	4.39	0.045
Site × Size	1	0.01	0.21	0.650
Treatment × Site × Size	1	0.00	0.00	0.954
Residual	30	0.01		
Margaleff's *M* (log 10)				
Treatment	1	0.24	131	**0.000**
Site	1	0.08	45.2	**0.000**
Size	1	0.00	0.09	0.771
Treatment × Site	1	0.03	19.2	**0.000**
Treatment × Size	1	0.01	0.56	0.461
Site × Size	1	0.01	0.81	0.377
Treatment × Site × Size	1	0.00	0.19	0.665
Residual	30	0.01		

[a] Significant values (after Bonferroni correction) are in bold.

Cerastoderma edule (L.), *Macoma balthica* (L.) and *Retusa obtusa* (Montagu), and the polychaetes *Pygospio elegans* (Claparède) and *Nephtys hombergii* (Savigny). Site had a significant affect on abundances of tubificid oligochaetes, and on the polychaetes *Streblospio benedictii* (Webster) *Nephtys hombergii* and *Capitella capitata* (Fabricius).

3.2. Multivariate analyses

Cluster analysis places samples into discrete groups according to their community

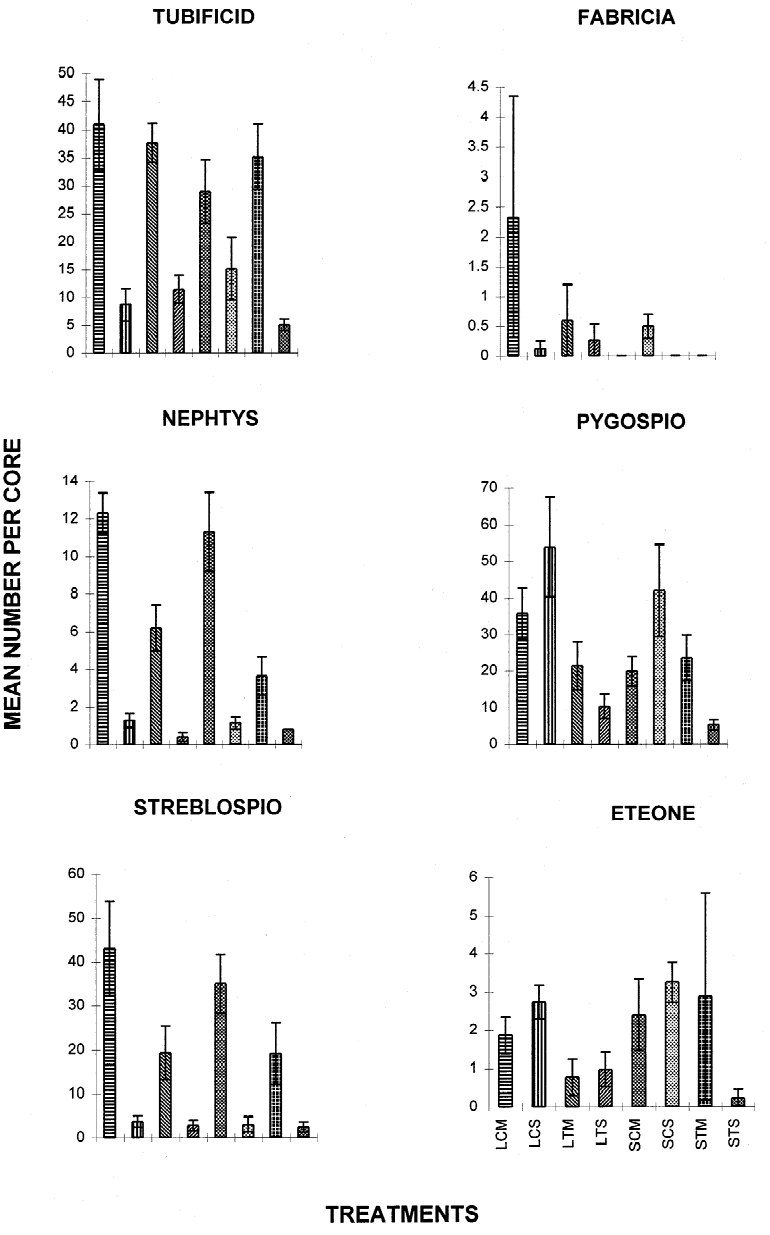

Fig. 2. Mean abundances per core of the dominant macroinvertebrates recovered from all treatments, with 95% confidence intervals. Legend key: LCM, large control mud; LCS, large control sand; LTM, large treatment mud; LTS, large treatment sand; SCM, small control mud; SCS, small control sand; STM, small treatment mud; STS, small treatment sand.

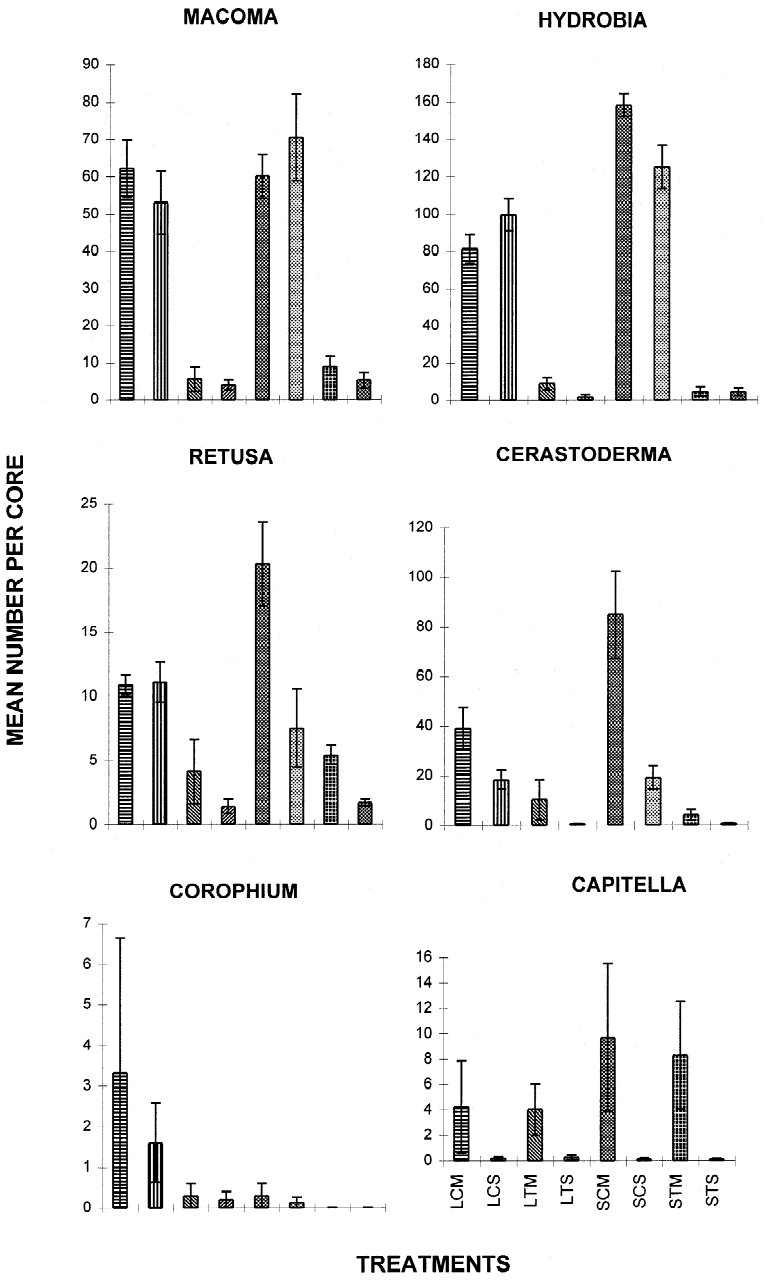

Fig. 2. (*continued*)

Table 2
Three-way analysis of variance of taxa abundance in all treatments, with interaction terms[a]

Source	df	MS	*F*	*P*
Hydrobia				
Treatment	1	18.5	159	**0.001**
Site	1	0.05	0.48	0.495
Size	1	0.18	1.58	0.219
Treatment × Site	1	0.16	0.92	0.345
Treatment × Size	1	0.76	0.61	0.442
Site × Size	1	0.01	0.08	0.778
Treatment × Site × Size	1	0.15	1.25	0.273
Residual	31	0.12		
Macoma				
Treatment	1	10.9	173	**0.000**
Site	1	0.55	0.87	0.359
Size	1	0.12	1.84	0.184
Treatment × Site	1	0.03	0.50	0.484
Treatment × Size	1	0.03	0.52	0.475
Site × Size	1	0.01	0.08	0.777
Treatment × Site × Size	1	0.06	1.01	0.322
Residual	32	0.06		
Cerastoderma				
Treatment	1	11.6	120	**0.000**
Site	1	1.95	20.1	**0.000**
Size	1	0.03	0.30	0.587
Treatment × Site	1	0.01	0.01	0.90
Treatment × Size	1	0.13	1.39	0.248
Site × Size	1	0.01	0.18	0.677
Treatment × Site × Size	1	0.17	1.79	0.190
Residual	31	0.10		
Retusa				
Treatment	1	2.31	61.3	**0.000**
Site	1	0.69	18.2	**0.000**
Size	1	0.01	0.32	0.579
Treatment × Site	1	0.02	0.43	0.515
Treatment × Size	1	0.01	0.31	0.585
Site × Size	1	0.19	5.16	*0.030*
Treatment × Site × Size	1	0.06	1.74	0.197
Residual	30	0.04		
Capitella				
Treatment	1	0.03	0.18	0.677
Site	1	2.6	15.3	**0.000**
Size	1	0.11	0.64	0.429
Treatment × Site	1	0.01	0.09	0.764
Treatment × Size	1	0.00	0.05	0.819
Site × Size	1	0.16	0.98	0.330
Treatment × Site × Size	1	0.00	0.00	0.960
Residual	30	0.17		
Eteone				
Treatment	1	0.55	8.82	**0.006**
Site	1	0.03	0.50	0.486
Size	1	0.02	0.34	0.563

Table 2. Continued

Source	df	MS	*F*	*P*
Treatment × Site	1	0.01	0.24	0.060
Treatment × Size	1	0.00	0.14	0.708
Site × Size	1	0.01	0.20	0.658
Treatment × Site × Size	1	0.00	0.00	0.950
Residual	30	0.06		
Nephtys				
Treatment	1	0.62	18.6	**0.000**
Site	1	4.17	123	**0.000**
Size	1	0.02	0.68	0.418
Treatment × Site	1	0.09	2.87	0.101
Treatment × Size	1	0.01	0.04	0.838
Site × Size	1	0.07	2.05	0.162
Treatment × Site × Size	1	0.03	0.99	0.327
Residual	30	0.03		
Pygospio				
Treatment	1	1.84	21.6	**0.000**
Site	1	0.10	1.24	0.274
Size	1	0.13	1.49	0.232
Treatment × Site	1	0.92	10.9	**0.002**
Treatment × Size	1	0.05	0.60	0.445
Site × Size	1	0.03	0.31	0.579
Treatment × Site × Size	1	0.09	1.15	0.292
Residual	30	0.09		
Streblospio				
Treatment	1	0.39	2.57	0.119
Site	1	7.09	47.2	**0.000**
Size	1	0.03	0.23	0.634
Treatment × Site	1	0.31	2.03	0.164
Treatment × Size	1	0.02	0.16	0.691
Site × Size	1	0.09	0.61	0.441
Treatment × Site × Size	1	0.01	0.13	0.719
Residual	30	0.15		
Tubificidii				
Treatment	1	0.01	0.23	0.632
Site	1	3.09	63.9	**0.000**
Size	1	0.05	1.21	0.281
Treatment × Site	1	0.06	1.28	0.267
Treatment × Size	1	0.09	1.93	0.175
Site × Size	1	0.01	0.06	0.810
Treatment × Site × Size	1	0.22	4.49	0.043
Residual	30	0.05		
Corophium				
Treatment	1	0.15	2.13	0.155
Site	1	0.00	0.01	0.944
Size	1	0.17	2.41	0.131
Treatment × Site	1	0.00	0.00	0.969
Treatment × Size	1	0.04	0.57	0.456
Site × Size	1	0.01	0.02	0.896
Treatment × Site × Size	1	0.01	0.06	0.811
Residual	30	0.07		

[a] Significant values (after Bonferroni correction) are in bold.

similarity. Data from control cages in the sandy and muddy sites form clusters with 70% Bray–Curtis similarity (Fig. 3). Within the next largest group a third distinct cluster is shown by the treatment cages on the muddy site, with 54% similarity to the control

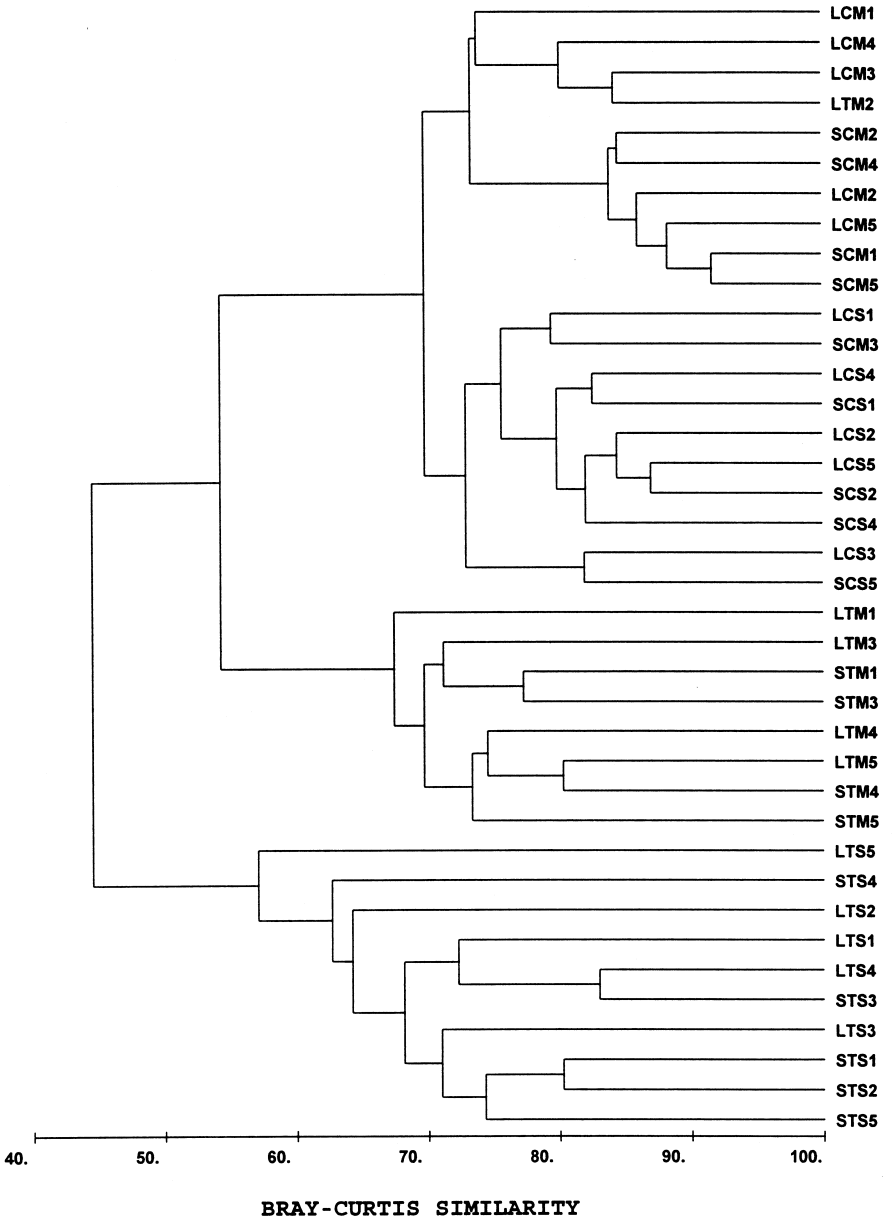

Fig. 3. Cluster analysis of macroinvertebrate abundance data, showing Bray–Curtis similarities after square root transformation.

cages. The interaction between predation and site is clearly shown by the fourth cluster, of treatment cages on the sandy site, which is only 44% similar to the other clusters (Fig. 3). Overall, communities in treatment cages on the muddy site were more similar to those in the control cages (muddy and sandy) than to the communities in the treatment cages on the sandy site.

Since clustering techniques are less useful in the analysis of data where there is a steady gradation in community structure, ordination was also performed on the same data set. Results are presented in Fig. 4. As in Fig. 3, there is a clear separation between three main groups, namely, (i) controls (muddy and sandy), (ii) treatment mud, and (iii) treatment sand. However, a gradation from group (i) to group (iii) through group (ii), which was not shown in the dendrogram (Fig. 3), is now evident.

In addition, it is apparent from Figs. 3 and 4 that there were no significant differences in community structure between large and small cages, for controls and treatments, in both sites. Results from ANOSIM (global R statistic, global p value, pairwise R values and pairwise p values) reinforced and confirmed statistically the main patterns observed in the ordination plot (Fig. 4). Significant differences ($p < 0.05$) were obtained by ANOSIM for all pairwise comparisons except for those between large and small treatments within the other treatment categories. Because there were a total of 28 pairwise comparisons, there is considerable risk of type I error. The magnitude of differences between treatments, therefore, is better represented by the pairwise R values (the statistic produced by ANOSIM), rather than the p values obtained (Dr K.R. Clarke, pers. commun.). Four pairwise comparisons are possible between each pair of treatment categories if cage size is disregarded (e.g. large control mud (LCM) vs. small control

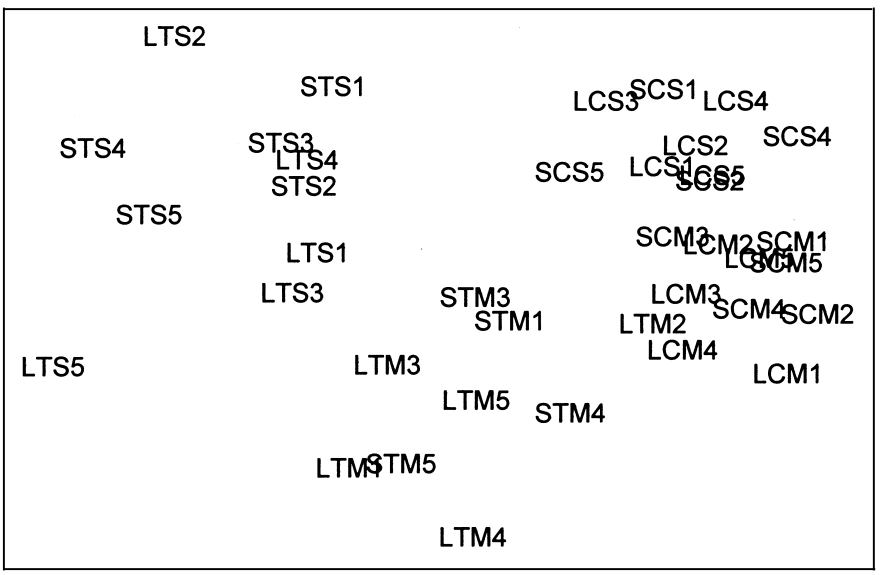

Fig. 4. Non-metric multi-dimensional scaling (MDS) ordination of macroinvertebrate abundances. Stress = 0.1.

Table 3
Median R values from ANOSIM pairwise tests ($n = 4$)[a]

Groups compared	Median R value
Control mud vs. treatment sand	0.996
Control sand vs. treatment sand	0.954
Control sand vs. treatment mud	0.895
Control mud vs. treatment mud	0.817
Treatment mud vs. treatment sand	0.715
Control mud vs. control sand	0.664

[a] An R of 1 implies that all replicates within a group are more similar to each other than to any replicates in the other group.

sand (SCS), LCM vs. LCS, SCM vs. LCS and SCM vs. SCS). Median R values for these comparisons are presented in Table 3. There are significant differences between these (Kruskal–Wallis test, $H = 1496$; df = 5, $p = 0.01$). The median R values confirm that the largest differences occurred between control mud and treatment sand groups (median R of 0.996; an R value of 1 implies maximum possible difference), with the smallest differences between the two controls, sand and mud (median R of 0.664).

4. Discussion

Our results indicate that the impacts of crab predation were similar in the different cage sizes (different spatial scales) but different on the different sites (habitat difference).

Field experiments, often involving caging, are the most reliable way of assessing the importance of predators in many marine systems (Hall et al. 1990a). However, previous caging work involving invertebrate epibenthic predators in soft-sediment habitats has given conflicting results. For example, Scherer and Reise (1981) and Gee et al. (1985) report significant effects of *Carcinus* on macrobenthic communities. In contrast, Thrush (1986), Frid and James (1988) and Raffaelli et al. (1989) found *Carcinus* had little impact (apart from on *Hydrobia ulvae*), and Hall et al. (1990b) found little evidence that the related crab *Liocarcinus depurator* (L.) affected community structure.

The present study showed a large impact of *Carcinus* on the macrobenthos. The densities of crabs used in this experiment were deliberately high (48 per m^2, compared to an estimated maximum natural density of similar sized crabs of five per m^5), since measuring the importance of crab predation at this site was not the primary purpose of this work. However, this result is noteworthy given the number of crabs used in the Raffaelli et al. (1989) study; although their high density treatment enclosed 10–15-mm carapace width crabs at 90 per m^2, they report few effects. The discrepancies between the studies cited here cannot, therefore, simply arise from different enclosure densities, since densities in the present work (and those in Gee et al., 1985) were less than in Raffaelli et al. (1989).

Instead, it is possible that the effects of *Carcinus* on soft-bottom community structure are location-specific (and possibly time-specific too). This might arise for at least two reasons. First, where individuals of susceptible prey species, such as molluscs, constitute

a large proportion of all species in a community, crabs might be expected to have a large impact since they are their preferred prey. *Hydrobia ulvae* was the only mollusc species found by Raffaelli et al. (1989) (although by using a 500-μm sieve they might have missed newly settled mollusc spat). Second, differences in the physical structure of the habitat might change how efficiently crabs forage for their prey (Eggleston et al., 1992), and how susceptible prey are to predators (Irlandi, 1994; Irlandi et al., 1995). Alternatively, the results of these studies might conflict because of differing caging artefacts caused by the use of different experimental designs. In particular, different sizes of cage might lead to different probabilities of detecting a significant predator effect.

A number of authors have warned about the potential for prey movement to confound the effects of predators in caging experiments (Frid and James, 1988; Hall et al., 1990a; Englund and Olsson, 1996; Englund, 1997). The Englund (1997) analysis suggests that this problem will increase as cage size decreases. He concludes that the results of small-scale experiments are likely to reflect prey movement rates, rather than any impacts of predation, and cautions that it is not possible to extrapolate the results of such caging experiments to larger scales. This is unwelcome news to most fieldworkers, who usually conduct their experiments precisely in order to suggest the importance of predators in the habitat as a whole. The relevant question is therefore 'What size corresponds to *small-scale* (in Englunds' sense) in the habitat of interest?'. The answer depends on the rate of prey movement; if this is small (such as on rocky shores) then cages can be small. Unfortunately, knowledge of prey movement rates in soft-sediment communities is not sufficient to allow a priori predictions of the correct cage size for most prey species (Hall et al., 1990a). It is therefore possible that many of the studies which report weak or no effects of predation in soft-sediments have been confounded by prey movement. If this is true, ecologists' understanding of the general importance of predation in such systems would need revision, and the advice given by Hall et al. (1990b) that experimenters should use a large number of replicate cages would require a caveat; experimenters would also require a large *size* of cage, which might affect the number of replicates that could be used. Alternatively, workers could use closed designs, which do not allow prey movement, but these would inevitably involve exacerbating hydrodynamic artefacts, and could change prey behaviour.

The present study found no effects of cage size on community or population responses to predation. This suggests that, for this particular predator–prey system in this particular habitat, it is possible to apply the results from experiments conducted with cages of at least 0.25 m^2 size to 1 m^2. Although such extrapolation must always be done carefully, Englund's advice that it is generally not possible is over-cautious. Rates of prey movement were clearly not sufficient to confound the large impacts of crab predation at this scale. It is still possible that both our small and large cage sizes were too small; had we used even larger enclosures, we may have found significant impacts on species which were apparently unaffected in the present study. This is unlikely, however, for two reasons. First, the most heavily impacted prey species (the molluscs) were also probably the most mobile; large numbers of juvenile bivalves in particular, move into and out of a square meter of sediment at this site on each tide (M. Richards, pers. commun.). Second, the common species which showed no signs of being affected

by crab predation, *Capitella* and tubificids, are not recorded as prey species for juvenile *Carcinus* (Raffaelli et al., 1989). We therefore conclude that a cage size of 0.25 m^2 is sufficiently large in this habitat to avoid confounding effects by prey movement in predation experiments. Interestingly, our results suggest that in some cases small cages may be preferable to large ones. The survival rate of crabs was higher in our small cages, perhaps because the small cages had a larger edge/area ratio than the large, and most crabs in both sizes of cage were recovered buried next to the edge. Hence, the behaviour of predator species is a consideration of equal or greater importance in deciding the design of cages than the movement rates of prey.

Artefacts such as increased sedimentation, caused by the hydrodynamic impacts of cages, are always of concern in caging experiments. Unfortunately, differences in sediment type between cages could not be tested for in the present work. However, we do not believe that such artefacts had a major impact on our results. Crab enclosure work carried out on the same site, using the same cage design, showed no significant differences in sediment characteristics between treatments after running for 10 days longer than the current study (M. Richards, pers. commun.).

Although changing cage size (or grain, in the Thrush et al. (1997) terminology) had no effect, changing the extent of the experiment, by including a different site, did affect results. Both univariate and multivariate analyses show clear interactions between treatment and site.

Our two sites were chosen as having high biological similarity; this is reflected in the closeness of the sandy and muddy control replicates on the MDS plot (Fig. 4). Crab predation had a greater impact in the sandy than the muddy site. The MDS and Bray–Curtis analyses show that the treatment mud communities were more similar to the control communities than to the treatment sand communities. Crab predation caused a significantly greater percentage reduction in the total number of all individuals, and a greater reduction in the number of species, in the sand than in the muddy site. One explanation for this difference is that it reflects different survivorship of crabs in cages on the two sites, i.e. it represents an experimental artefact. Although mean survivorship of crabs was lower in the large, muddy treatment than in the large sandy treatment (as a result of two large cages on the muddy site with anomalously low survivorship), it was exactly the same in the small cage treatments at both sites. Since none of our analyses suggest any differences between small and large treatments, we do not believe that different crab survivorship explains the differences between sites. Rather, it is possible that mud habitats afford refuges for the crabs' preferred prey, which are not available in sandy habitats. Eggleston et al. (1992) found significantly higher mortality rates of *Macoma balthica* under predation by blue crabs (*Callinectes sapidus* (Rathbun)) in sandy compared with muddy sediment, probably because *Macoma* live at deeper depths in muddy sediment. This depth refuge in mud could be relevant for some or all of the other prey species in the present study. Nematode communities in sandy sediments are also more affected by *Carcinus* predation than those in muddy sediments (Schratzberger and Warwick, 1998), possibly because of greater competition between crabs and other, infaunal predators for food in sandy compared with mud sediments.

Although mollusc spat (particularly *Macoma* and *Cerastoderma*) settle in both muddy and sandy sediment at Blackness, larger populations of adults are found in sandy sites (M. Richards, pers. commun.). This distribution is the opposite of what is expected given

the results of the present study; the greater foraging efficiency of crabs on sand should result in higher prey densities in muddy sediment. Understanding how predation structures macrobenthic communities at this site clearly requires a combination of approaches, and this anomaly further illustrates the need to treat the results of caging experiments with caution. It is possible that the crabs' own predators forage more efficiently in the sandy habitats, thus excluding the crabs (who were artefactually protected in this work).

In conclusion, the present work demonstrates the importance of scale in interpreting the results of caging experiments, but at the level of extent, rather than grain (Thrush et al., 1997). Rates of prey movement are not sufficient in this habitat to obscure predator impacts with experimental cages of at least 0.25 m^2 size. Of more concern, as a source of artefacts, are possible alterations in predator behaviour involved in caging. Caging experiments remain one of the most powerful ways in which to explore predator–prey interactions. However, the confident interpretation of their results requires a detailed knowledge of the natural distribution and behaviour of the predator, and an appreciation of how subtle characteristics of habitat can influence predator–prey dynamics.

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