

1 **Assessing the impacts of bait collection on inter-tidal sediment and the associated**  
2 **macrofaunal and bird communities: the importance of appropriate spatial scales.**

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4 **Running head: the impacts of bait collection**

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28 **Abstract**

29 Bait collection is a multibillion dollar worldwide activity that is often managed  
30 ineffectively. For managers to understand the impacts on protected inter-tidal  
31 mudflats and waders at appropriate spatial scales macrofaunal surveys combined  
32 with video recordings of birds and bait collectors were undertaken at two UK sites.  
33 Dug sediment constituted approximately 8% of the surveyed area at both sites and  
34 is less muddy (lower organic content) than undug sediment. This may have  
35 significant implications for turbidity. Differences in the macrofaunal community  
36 between dug and undug areas if the same shore height is compared as well as  
37 changes in the dispersion of the community occurred at one site. Collection also  
38 induces a 'temporary loss of habitat' for some birds as bait collector numbers  
39 negatively correlate with wader and gull abundance. Bait collection changes the  
40 coherence and ecological structure of inter-tidal mudflats as well as directly  
41 affecting wading birds. However, as  $\beta$  diversity increased we suggest that  
42 management at appropriate hectare/site scales could *maximise*  
43 biodiversity/function whilst still supporting collection.

44

## 45 **1. Introduction**

46 Invertebrate species are increasingly exploited for human use with a dramatic rise in  
47 catch levels in recent decades (Anderson et al., 2011a), but not all are collected for  
48 food. Polychaete bait is an integral part of coastal life, but is perceived as a low  
49 value resource as fisheries are data-limited, locally focussed, and largely  
50 unregulated. However, a recent assessment has shown that the global catch is  
51 approximately 121,000 tonnes per annum with a retail value of £5.5 billion (Watson  
52 et al., 2017). This is comparable to many of the world's most important fisheries, but  
53 in addition, productivities (i.e. biomass removed per m<sup>2</sup> of inter-tidal sediment) are  
54 orders of magnitude greater than many sub-tidal invertebrate fisheries (Watson et  
55 al., 2017).

56 In many locations ragworms are the major group collected from inter-tidal soft  
57 sediment shores with *Alitta (Nereis) virens* one of the most important species in  
58 Europe and the USA (Olive, 1994). For example, the UK fishery alone for this species  
59 is estimated to be 1500 t per annum (Watson et al., 2017). *A. virens* is a keystone  
60 inter-tidal species as prey for fish, birds and crustaceans; as a predator of other  
61 invertebrates and as an important bioturbator (McIntosh 1908-1910; Ambrose,  
62 1986; Ambrose et al., 1998; Caron et al., 2004). Many studies have investigated the  
63 impacts of collecting a variety of bait species including lugworms (Blake, 1979;  
64 McLusky et al., 1983; van den Heiligenberg, 1987; Olive, 1993; Harvard and Tindal  
65 1994; Beukema, 1995); bloodworms (Brown and Wilson, 1997; Ambrose et al., 1998;  
66 Beal and Vencile, 2001; Miller and Smith, 2012) and shrimps (Contessa and Bird,  
67 2004; Skilleter et al., 2005; 2006; Winberg and Davis, 2014). Several have also  
68 investigated the impacts of sediment disturbance from other invertebrate inter-tidal  
69 fisheries (e.g. Beal and Vencile, 2001; Kaiser et al., 2001; Dernie et al., 2003; Logan,  
70 2005; Griffiths et al., 2006; Masero et al., 2008; Navedo and Masero, 2008). Whilst  
71 all have shown impacts, the responses have been inconsistent; underlining the  
72 difficulty of extrapolating results across systems (e.g. different target species and  
73 source habitats). For those that have assessed ragworm collection (Blake, 1978;  
74 Olive, 1993; Brown and Wilson, 1997; Watson et al., 2007) and for many of the other  
75 studies, the relevant spatial scales (hectares) that bait collection covers have not

76 been used. Instead, small experimental plots have been established, but these suffer  
77 considerable artefacts such as macrofaunal migration from surrounding areas and  
78 that recovery rates and size of the effect are related to the area of disturbance  
79 (Munari et al., 2006; Carvalho et al., 2013). In addition, collection areas often  
80 correlate with spatial coverage of MPAs (Marine Protected Areas) used as a  
81 management tool in coastal areas (Wood *et al.*, 2008). Surveys, therefore, assessing  
82 the impacts of ragworm collection on the macrofaunal community representative of  
83 the spatial scales (hectares) that bait collection covers are needed to support  
84 evidence-based management of these fisheries within MPAs.

85 The impacts of bait collection also extend to wading bird populations which may be  
86 affected by reductions in key prey species (Shepherd and Boates, 1999; Masero et  
87 al., 2008) or by the presence of collectors on the shore (i.e. disturbance). As  
88 disturbance results in either a loss of feeding time or increased energy expenditure,  
89 it has the potential to negatively affect energy balance and survival (Davidson and  
90 Rothwell 1993). A variety of coastal activities including bait collection can induce  
91 disturbance (e.g. Shepherd and Boates, 1999; Townshend and O'Connor, 1993;  
92 Ravenscroft et al., 2007; Liley and Fearnley, 2012; Stillman et al., 2012). However,  
93 for bait collection these studies were extremely limited in their scope because they  
94 a) simultaneously assessed multiple coastal activities; b) were not at the appropriate  
95 spatial scale or c) did not control for season and year.

96 In many locations bait collection remains a contentious issue for collectors, those  
97 organisations charged with minimising impact, and the associated coastal  
98 communities. Conservation legislation (e.g. European Union Natura 2000 sites)  
99 requires direct (Special Areas of Conservation [SACs]) and indirect (sub-features of  
100 Special Protection Areas [SPAs]) protection of inter-tidal mudflats to maintain them  
101 in favourable condition. In other words, subject to natural change, the range and  
102 distribution of characteristic biotopes and abundance of prey species for birds of  
103 interest must be maintained (English Nature, 2001). Overlap of protected coastal  
104 habitat and areas with high levels of collection gives great scope for conflict in many  
105 parts of the world. Effective management of bait collection in areas of protected  
106 inter-tidal mudflat (including areas protected for wading birds and wildfowl) requires

107 an understanding of these impacts. Using two popular UK collection sites within the  
108 Solent region (part of the Solent European Marine Site [SEMS]) as case studies we  
109 mapped the extent of dug areas and collected cores for macrofaunal and sediment  
110 analysis from multiple transects located in dug/undug and low and mid shore areas  
111 to test hypothesis one: 1. Collection of *A. virens* by digging will significantly alter the  
112 macrofaunal community and the associated sediment characteristics over large (i.e.  
113 MPA-relevant covering several hectares) spatial scales. Remote Closed Circuit  
114 Television [CCTV] cameras were then used to record the numbers of collectors and  
115 abundance and diversity of birds on the inter-tidal sediment to test hypothesis two:  
116 2. The presence of collectors on the sediment will reduce the bird abundance of  
117 waders and wildfowl utilising the same location.

118

## 119 **2. Materials and Methods**

### 120 *2.1. Biotope surveys and sample collection*

121 Fareham Creek is a key bait collection area within the Portsmouth Harbour SPA  
122 (Fowler 2001). An additional MPA prohibiting commercial collection within the  
123 SNCO (Special Nature Conservation Order) has been in force since 2003/4 (Figure  
124 S1). Dell Quay in Chichester Harbour is also an important collection site (Fowler,  
125 2001), but it contains many intertidal moorings and jetties. Consequently, the local  
126 NGO implemented a byelaw to prohibit bait collection within 15 m of any mooring or  
127 6 m of any structure (Figure S2).

128

129 Each site was surveyed once on spring tides between August and September 2011  
130 approximately three hours either side of low tide. A biotope survey (Connor et al.,  
131 2004) assessment of the inter-tidal sediment (excluding the channels) was  
132 conducted and bait-collected areas mapped using a Differential Global Positioning  
133 System (DGPS) (approximately 10 cm accuracy) in conjunction with hand-drawings of  
134 habitat boundaries on aerial photographs (scale 1: 10000). Points were recorded by  
135 walking along the outer boundary of dug areas and any polygons considered too  
136 small to be mapped with DGPS, were numbered on the aerial photographs. Bait dug

137 areas matched in the field were then digitised in GIS (ArcMap) and compared with  
138 the MPA boundary areas and the total substrate mapped.

139 Bait dug areas were defined as those exhibiting characteristics based on our own  
140 observations and those of Coates (1983), Brown and Wilson (1997) and Fearnley et  
141 al. (2013). These included: uneven topography (the area has mounds, water-filled  
142 depressions and troughs); the presence of empty bivalve shells and stones on the  
143 surface; a lack of algal mat cover; and the presence of darker (anoxic) sediment on  
144 the surface. Turned over sediment can persist for variable lengths of time  
145 depending on the energy of the site (Coates, 1983; McLusky et al., 1983; Sypitkowski  
146 et al., 2010; Fearnley *et al.*, 2013). It was not possible to directly record the 'age' of  
147 the dug sediment from which cores were taken as collectors were not individually  
148 tracked. However, monthly assessment (January-June 2016) of four replicate 1 m<sup>2</sup>  
149 dug areas in the Solent intertidal area confirms dug sediment persists for 83 ± 30  
150 days SD in low energy shores. We, therefore, assumed that dug areas were dug a  
151 maximum of 12 weeks prior to sampling.

152 A systematic sampling strategy for macrofaunal and sediment analysis was  
153 performed with 10 transects at Fareham Creek (Figure S1) and 11 transects at Dell  
154 Quay (Figure S2) covering both nominally protected and unprotected areas. Four  
155 sampling stations (two mid-shore and two low-shore either side of the central  
156 channel) were located and at each one 0.01 m<sup>2</sup> (15 cm deep) core was taken and  
157 fixed in 10% formalin in seawater for faunal analysis. An additional 5 cm diameter  
158 core was taken at each station and frozen (-20°C) for future sediment analysis.

159

## 160 *2.2. Sample processing*

161 Sediment cores were heated at 60°C until completely dry and processed using wet  
162 sieving for particle size analysis and loss on ignition at 475°C for 4.5 hours for organic  
163 content (Buchanan, 1984). All cores (39 cores in total) from Fareham Creek and all  
164 except one from transect 7 (40 cores in total) for Dell Quay were analysed for  
165 sediment characteristics. Samples to be processed for macrofaunal analysis were  
166 chosen *a posteriori* according to the following scheme due to financial restrictions.

167 At Fareham Creek all cores from the low shore were processed except one  
168 unprotected from transect 4 due to its loss (19 cores in total). All cores (low and mid  
169 shore) for Dell Quay from transects 2 -10 except one from transect 10 were  
170 processed (35 cores in total) (see Figures S1 and S2).

171

### 172 *2.3. CCTV installation and video analysis for bird disturbance*

173 Two Sanyo HD 4600 cameras with external hard-drives were used for direct  
174 recording and were rotated between the sites (see Watson et al. [2015] for details),  
175 focussing on areas of the inter-tidal mudflat where previous observations had shown  
176 there to be significant collection. Only daylight tides were utilised and cameras were  
177 deployed twice at each site. The area of mudflat to be analysed was determined by  
178 firstly using topographical features to set the boundaries of the area. This trapezium  
179 was then measured on the ground whilst the camera was still operating. Six zones  
180 (due to the perspective they were varied sizes) were produced which made up the  
181 larger trapezium (see Table S1). At 10 minute intervals over three hours, birds were  
182 counted and identified (where possible) for one minute in each zone and if they  
183 were on the mud or water was noted. Bait collector activity was also recorded  
184 including the type of activity (digging, walking or washing equipment). Birds that  
185 were flying over a zone were not included, although those landing during the  
186 recording period were. Correspondence with the UK Government's Information  
187 Commissioner's Office confirmed that personal data legislation did not apply to the  
188 images collected.

189

### 190 *2.4. Data analysis*

191 Macrofaunal species abundance data were synonymised with the WoRMS (2016)  
192 database before excluding terrestrial and planktonic species. Univariate and  
193 multivariate methods (e.g. non-metric multi-dimensional scaling ordination based on  
194 a square root transformed Bray Curtis similarity matrix of species abundance)  
195 followed by SIMPER, PERMANOVA and CAP (Canonical Analysis of Principal

196 Components) were used, where appropriate, for the macrofauna data using PRIMER  
197 v 6.0 (Anderson and Willis, 2003; Anderson et al., 2008). Multivariate dispersion  
198 between dug and undug communities was assessed using the Index of Multivariate  
199 Dispersion (IMD) and PERMDISP routines. According to Anderson et al. (2006)  
200 PERMDISP is directly interpretable as a test for similarity in  $\beta$  diversity (defined as  
201 variability in composition) among groups when used on presence/absence data in  
202 conjunction with the Bray Curtis similarity matrix. Data were, therefore,  
203 transformed to presence/absence and analysed with this routine.

204 Particle size analysis was performed using the software package Gradistat Ver. 8.0  
205 (Blott and Pye 2001) with the geometric Folk and Ward (1957) method applied to  
206 produce a mean particle size. The Buchanan (1984) sieving method does not  
207 separate the proportion of material less than 63  $\mu\text{m}$  into smaller fractions.  
208 Therefore, all measures were calculated with the size of this fraction specified at 1  
209  $\mu\text{m}$  and this was then taken as being representative of the whole fraction.

210 Species number (S), number of individuals (n), Hill's N1 diversity index and sediment  
211 characteristics were analysed further using General Linear Models (including, if  
212 appropriate, protected/unprotected, dug/undug, transect, low/mid shore as factors)  
213 and transformed to meet any parametric assumptions as required. This was  
214 achieved for all analyses except Hill's N1 diversity index for Dell Quay as the  
215 variances could not be equalised. Models were run including interactions if the  
216 hierarchical structure of the data allowed. To achieve a simplified model,  
217 interactions were subsequently excluded if found not to be significant (Gardiner,  
218 1997; Crawley, 2007) and then the reduced and full models were compared using  
219 the adjusted deviance  $R^2$  to select the one with the best fit. Analysis of individual  
220 species abundances for Dell Quay were attempted with a variety of GLM (with  
221 transformation), Poisson and other regression models, but none provided an  
222 appropriate fit for the data. Consequently, only graphical presentations were  
223 employed to show these data. Correlations for bird abundance and bait collector  
224 activity were performed using a Pearson Correlation with the first seven days of data  
225 per site/view analysed to standardise the number of days between camera runs.

226



227 **3. Results**

228 *3.1. The effects of bait collection on sediment*

229 The area mapped at Dell Quay was nearly three times as large as Fareham Creek and  
230 surveys showed that dug sediment was present at both sites and constituted a  
231 sizable proportion (Fareham Creek: 8.2% [2.6 ha] and Dell Quay: 9.7% [8.1 ha],  
232 respectively) of the areas mapped. Of this dug sediment, 42% was recorded within  
233 the SNCO for Fareham Creek, but only 0.5% for Dell Quay was in the exclusion zones  
234 around moorings and jetties.

235 At the site level the predominant sediment description types for Fareham Creek  
236 were fine sand and coarse silt with an associated mean particle size ( $\pm$  SE) of  $396 \pm 93$   
237  $\mu\text{m}$ . Sediment particles were generally very poorly sorted, symmetrical in terms of  
238 skewness and leptokurtic. With a mean percentage level of mud of  $41 \pm 3.9$  % and  
239 relatively high organic content ( $5.16 \pm 0.5\%$ ) these conditions reflect the low wave  
240 energy and deposition shores typical of the region. However, variability between  
241 cores for all measurements was considerable; some cores had no particles classed as  
242 mud or smaller, whereas others had over 80% less than  $63 \mu\text{m}$ .

243 Principal sediment description types for Dell Quay were also fine sands with an  
244 associated overall site mean particle size of  $407 \pm 99 \mu\text{m}$ . Sediment particles were  
245 very poorly sorted, symmetrical in terms of skewness and very platykurtic for  
246 kurtosis. The mean percentage level of mud and organic content were  $33.7 \pm 2.7$  %  
247 and  $2.96 \pm 0.3\%$ , respectively. Variability between cores for all measurements was  
248 still present, but less so than at Fareham Creek.

249 To assess if there were any patterns to the sediment at each site from the factor  
250 assigned to the core, GLMs were performed (Table 2). As it was clear from the  
251 biotope survey of Fareham Creek that the MPA (protection) had not been successful  
252 in preventing collection (42% of the recorded dug sediment was within the SNCO),  
253 therefore, only dug/undug, transect and height on shore were used as factors for the  
254 sediment analysis. Analyses of the organic content confirmed there were no  
255 significant differences between transects ( $F= 1.63$ ,  $p=0.154$ ) or height on shore  
256 (Table 2). However, dug and undug areas did differ; undug areas had a significantly

257 higher organic content. For the particle size datasets the low shore areas had a  
258 significantly higher mean particle size.

259 As less than 0.5% of the dug area was recorded within the protected zones at Dell  
260 Quay we have judged it to have been successful and, therefore, included  
261 protected/unprotected as well as dug/undug, transect and height on shore as factors  
262 for analysis (Table 2). Sediment characteristics at Dell Quay were much more  
263 dependent on the factor assigned to the core. Organic content was significantly  
264 higher in the undug areas; and significant differences were also present between  
265 transects ( $F= 4$ ,  $p=0.002$ ), but no significant differences between particle size and  
266 percentage of sediment classified as mud for any factor except transect ( $F =3.15$ ,  $p$   
267  $=0.028$ ,  $F =3.12$ ,  $p =0.029$ , respectively) were recorded.

268

### 269 3.2. Macrofaunal diversity

#### 270 Fareham Creek

271 At a site level (across all cores) seven taxon dominated the site (nematodes, *Tharyx*  
272 *sp.*, *Peringia ulvae*, *Streblospio spp.*, *Tubificoides benedii*, *T. pseudogaster* [agg] and  
273 *Baltidrilus costatus*) accounting for 95.6% of the total number of individuals  
274 recorded. These species contributed the vast majority of the percentage total for  
275 each core, in some cases up to 97% of the species abundance. When compared  
276 between factors (dug/undug and transect) using GLMs, no significant differences  
277 were found for  $S$ ,  $n$  and Hill's  $N1$  (Table 3). A PERMANOVA test did record a  
278 significant difference between the community, but across transects only (pseudo  $F =$   
279  $1.76$ ,  $p = 0.013$ ) and this is supported by a non-metric multi-dimensional scaling plot  
280 (Figure 3) with clear organisation across transects. Nevertheless, changes in the  
281 relative dispersion of the community (IMD) between dug and undug cores  
282 consistently showed greater variability in species compositional structure in undug  
283 locations and these differences were significant using PERMDISP, although they did  
284 not extend to  $\beta$  diversity (Table 4).

285

#### 286 Dell Quay

287 Four taxa (nematodes, *Tharyx* sp., *P. ulvae* and *T. benedii*) accounted for 75% of the  
288 total number of individuals recorded with one of these species accounting for up to  
289 90% in some cores. Univariate analyses of species abundance mainly showed no  
290 significant differences between the factors when analysed with General Linear  
291 Models except for Hill's N1 and S (Table 3). For S, cores from protected areas and  
292 the mid shore had significantly higher numbers of species (approximately four more  
293 species on average per core) with significant differences also between transects [F =  
294 3.58,  $p = 0.020$ ]. There were also significant interaction terms  
295 (protected/unprotected and dug/undug [F = 7.33,  $p = 0.018$ ]; protected/unprotected  
296 and height [F = 10.9,  $p = 0.006$ ]; and height and transect [F = 4.1,  $p = 0.013$ ]).  
297 Diversity (Hill's N1) was significantly higher in unprotected areas and there were also  
298 significant interaction terms (protected/unprotected and dug/undug [F = 6.7,  $p =$   
299  $0.023$ ]; protected/unprotected and height [F = 24.6,  $p > 0.001$ ]; and height and  
300 transect [F = 3.9,  $p = 0.017$ ]). Analysis using PERMANOVA with all factors  
301 (protected/unprotected, dug/undug, transect and height on shore) shows that  
302 significant community differences were present for all factors  
303 (protected/unprotected, pseudo F = 2.94,  $p = 0.013$ ; dug/undug, pseudo F = 4.12,  $p =$   
304  $0.006$ ; transect, pseudo F = 1.87,  $p = 0.015$ ; and height on shore, pseudo F = 2.96,  $p =$   
305  $0.024$ ) in addition to a significant interaction for transect and height on shore (F =  
306 1.81,  $p = 0.037$ ). Changes in the relative dispersion of the community (IMD) between  
307 dug and undug cores confirmed greater variability in species compositional structure  
308 in undug locations. These changes were not significant when analysed using  
309 PERMDISP for Dell Quay alone, but were when the sites were combined (Table 4).  
310 No significant differences between protected and unprotected, and shore height  
311 were present as measured by PERMDISP (data not shown). Significant differences in  
312  $\beta$  diversity between dug and undug cores were also seen for Dell Quay and when  
313 both sites were combined.

314 It is important for the interrogation of digging effects to first reduce the influence of  
315 protection. To facilitate further analysis all cores collected from protected areas  
316 were excluded and the remaining data reanalysed with CAP. Figure 4 confirms that  
317 the canonical axes separate the dug from the undug sites, but also those from low

318 and mid shore. This clearly shows an impact of digging on the macrofaunal  
319 community, but also height on shore was important in determining the community  
320 response (the importance of both variables is confirmed by the permutation trace  
321 statistic of 2.42,  $p = 0.001$ ). SIMPER analysis was used to investigate which species  
322 contribute most to the dissimilarity between dug and undug cores. Average  
323 dissimilarity was 64.9, but the difference is again with contributions from a large  
324 number of species. For example, five of the most abundant species contributed only  
325 52% of the dissimilarity. To explore which species might be important the mean  
326 abundance for the 12 most common species from these cores are plotted split  
327 between: dug, undug, low and mid shore (Figure 5). Although there were some  
328 notable exceptions e.g. *Tharyx* sp., *Cyathura carinata* and *Corophium volutator*, the  
329 mid shore dug cores had consistently lower abundances than their undug  
330 counterparts. However, for the dug low shore cores only half the species had lower  
331 or similar abundances to undug cores (*P. ulvae*, *T. benedii*, *Capitella* spp., *C.*  
332 *volutator*, *Melita palmata*, *Austrominius modestus*, and *T. amplivasatus*).

333

### 334 3.3. Disturbance to birds

335 Bird numbers were recorded in each of the six zones alongside the number of bait  
336 collectors who were digging, washing equipment and walking. All six zones for each  
337 view were combined for analysis and the numbers of collectors per time point were  
338 correlated with the total number of birds and specific sub groups. (Whether a bird  
339 was on the mud or in the water was also combined for the analysis). These  
340 correlations and their associated statistical significance are presented in Table 5 for  
341 each camera view except Fareham Creek view 1 which was not analysed due to very  
342 low collector activity. There were considerable differences between numbers of  
343 birds and collectors recorded within and between camera views with two  
344 relationships significant (waders and gulls for Dell Quay camera views 1 and 3,  
345 respectively). Red shank (*Tringa totanus*), curlew (*Numenius arquata*), oystercatcher  
346 (*Haematopus ostralegus*), grey plover (*Pluvialis squatarola*) and dunlin (*Calidris*  
347 *alpina*) were identified and comprised the wader group from Dell Quay 1 view. Gulls  
348 were not identified to species for Dell Quay view 3

349 .

## 350 **4. Discussion**

### 351 *4.1 Bait collection at the sites*

352 The collection of bait can include a number of species from a range of phyla (Olive,  
353 1994; Watson et al., 2017). At both sites all collecting activity was for *A. virens*  
354 reflecting the species identified as most popular by Fowler (2001) for the Solent and  
355 extensively collected in Europe and the USA (Watson et al., 2017). Seasonal  
356 variations in effort and between sites are common for bait collection (Fowler, 2001;  
357 Sypitkowski et al., 2010; Miller and Smith, 2012). Nevertheless, as only one sampling  
358 period recorded nearly 10% of inter-tidal sediment as dug, the data presented  
359 confirms the continued importance of both sites as reported by Fowler in 2001 and  
360 shows bait collection to be a major activity in the SEMS MPA.

361

### 362 *4.2. Effects of protection and shore height*

363 The data from the walkover survey confirms that for Dell Quay the MPA byelaw  
364 excluding digging around moorings and jetties has been extremely successful with  
365 only a very small percentage of dug sediment recorded in protected areas in contrast  
366 to Fareham Creek. Watson et al. (2015) suggested that these divergent responses  
367 were due to successful sustained face-to-face conversations with collectors  
368 (unofficial enforcement) at Dell Quay rather than relying solely on passive education  
369 (e.g. signage at Fareham Creek).

370 All univariate measures except *n* (total number of individuals) were higher in the low  
371 shore area for Dell Quay, although only differences in the number of recorded taxa  
372 (*S*) were statistically significant. Differences in community structure between shore  
373 heights are not surprising considering benthic invertebrate biomass changes with  
374 emersion time (e.g. Beukema, 1976; Griffiths et al., 2006). It is likely that the  
375 different sediment characteristics between low and mid shore areas at Dell Quay  
376 are, in combination with physical variables that vary with shore height, responsible  
377 for the differences in community structure.

378 At Dell Quay the exclusion zones round moorings and jetties were successful in  
379 preventing collection, but resulted in increases in numbers of species (S) and  
380 diversity (Hill's N1 index) in addition to a change in the macrofaunal community (as  
381 measured by PERMANOVA). As other influences are confounded with protection  
382 further work is required to understand the interaction of the different processes.  
383 Scouring of the sediment by buoy-attachment chains reduces the median sediment  
384 particle size and changes the macrofaunal community and abundance of certain  
385 species (Herbert et al., 2009). As the majority of cores within protected areas came  
386 from areas close to boat moorings rather than jetties, scouring is likely to be  
387 responsible for the effects of protection. It is, therefore, important to consider the  
388 integration of bait exploitation management with management of existing site-  
389 specific activities (e.g. recreational boating) to ensure that they are additive in their  
390 effects.

391

#### 392 *4.3. Effects of bait collection*

393 Data presented here show for the first time that changes occur in the sediment and  
394 macrofaunal communities over large spatial scales when ragworms are collected for  
395 bait. Significant differences between dug and undug sediment were restricted to  
396 organic content, and for Dell Quay mean particle size was also lower in undug areas,  
397 although not significantly so. Together these show that undug sediment was  
398 muddier with a higher organic content and, in contrast to Carvalho et al. (2013), the  
399 response is generally not site-specific. Turning over the sediment changes the  
400 microtopography leading to the loss of the finer fractions and associated organic  
401 material as it is washed away by tides and wave action. This is likely to have  
402 important implications for local sediment load and turbidity levels. In addition, as  
403 organic matter binds many contaminants (Eggleton and Thomas, 2004) and sediment  
404 disturbance leads to desorption of pollutants (Edge *et al.*, 2015), an increase in  
405 bioavailability from bait collection is highly likely as shown by Howell (1985) for  
406 cadmium. The impacts of collection may, therefore, go well beyond the extent of  
407 dug sediment.

408 The distribution of benthic assemblages is known to relate to sediment  
409 characteristics (Snelgrove and Butman, 1994), but the responses to bait collection  
410 were site specific. At Fareham Creek the sediment changes observed did not result  
411 in significant changes to the macrofaunal community, although a significant increase  
412 in variability was recorded for dispersion. The significant differences in community  
413 structure between transects indicate the presence of a gradient down the creek  
414 (likely to be related to the freshwater input) and could have masked any digging-  
415 induced changes. Transect differences may also have been responsible for the  
416 reduction in variability for dug sites, but the number of replicates per transect  
417 precluded an analysis for this factor. Contrary to the influence of location (i.e.  
418 freshwater input) at Fareham Creek, the gradient at Dell Quay did not mask the  
419 changes seen at that site measured by PERMANOVA. In contrast to Fareham Creek,  
420 collectors at Dell Quay spent the majority of their time digging in areas that had  
421 already been dug (Watson et al., 2015). The cumulative impacts of repeated digging  
422 such as preventing recovery of small macrofauna species (Brown and Wilson, 1997)  
423 may have been sufficient for the differences to manifest themselves in the sediment  
424 and through to the macrofaunal community at Dell Quay.

425 According to Clarke and Gorley (2006) diversity indices are unable to detect subtle  
426 changes in a complex community and this is supported by the general lack of  
427 significant differences in GLMs for the univariate measures. In contrast, multivariate  
428 analyses show for the first time that 'natural levels' of hand-collection for *A. virens*  
429 produce significant changes in the macrofaunal community evident over large  
430 (hectares) spatial scales, in addition to responding to environmental factors such as  
431 shore height and location within the site (transect position). Responses of benthic  
432 species to disturbance often vary (e.g. McLusky et al., 1983; Harvard and Tindal,  
433 1994; Whomersley et al., 2010; Carvalho et al., 2013) and this was the case here.  
434 Increases in the abundance of *Tharyx* sp., *C. carinata* and *C. volutator* in dug areas on  
435 the mid shore and nematodes, *Tharyx* sp., *T. pseudogaster*, *Capitella* spp.,  
436 *Streblospio* spp. and *C. carinata* on the low shore contrast with large reductions in *P.*  
437 *ulvae*, nematodes and *T. benedii* for the mid shore and smaller reductions for *M.*  
438 *palmata* and *E. modestus* for the low shore areas (Figure 5). Brown and Wilson

439 (1997) and Masero et al. (2008) suggested that small surface-dwelling species are  
440 sensitive to disturbance, and Whormersley et al. (2010) showed that different  
441 disturbance types and intensities could change the trophic group ratios within a  
442 community. However, even these more broad-scale responses were still site and  
443 disturbance type specific. Our data also show that responses were not consistent  
444 between species (e.g. *C. volutator* and *P. ulvae*) or even between those within the  
445 same trophic group (e.g. *T. benedii* and *T. pseudogaster* as sub-surface deposit  
446 feeders; *C. volutator* and *Streblospio* spp. as surface deposit feeders). One  
447 explanation for this inconsistency is that, although we classified all dug sediment as  
448 being dug within 12 weeks of sampling, small species may recover in this timeframe  
449 leading to an increase in heterogeneity. Increased heterogeneity related to stress  
450 has been shown to occur for macrobenthos and other communities (Warwick and  
451 Clarke, 1993), although this is not supported by the IMD values or the PERMDISP  
452 analyses as both show a reduction in community variability in areas that are dug.  
453 Future work should include a method of assessing the age of dug sediment,  
454 however, the fact that differences between dug and undug sediment were present  
455 despite any partial recovery would suggest an even stronger response if dug  
456 sediment of the same age was compared. Our data, therefore, support our first  
457 hypothesis that collection alters the macrofaunal community and the associated  
458 sediment characteristics across large spatial scales, but with the caveat that the  
459 strength (and type) of the response is site specific. This is corroborated by data from  
460 Whormersley et al. (2010) who suggested that sites respond differently, not simply  
461 because of differences in species or trophic group, but because of inherent  
462 ecological plasticity exhibited by many benthic species (Davic, 2003) combined with  
463 history of prior disturbance.

464 Bait collection adds another layer of variation to already spatially diverse inter-tidal  
465 benthic systems where communities are influenced by site, height on shore and the  
466 presence of built structures as well as many other anthropogenic effects. Bait  
467 collection at these sites, and more generally, is temporally variable (Fowler, 2001;  
468 Sypitkowski et al., 2010; Miller and Smith, 2012; Watson et al., 2015). Combined  
469 with the spatial variability (patchiness) recorded here, sites where bait collection



470 occurs could be described as already heterogeneous areas overlaid with  
471 intermittently repeating disturbance at different spatial and temporal scales. In the  
472 context of the Intermediate Disturbance Hypothesis (Grime, 1973; Connell, 1978)  
473 this patchiness might lead to an overall increase in  $\beta$  diversity at the hectare/site  
474 scale. Inspection of the dispersion of the community data of cores from dug sites  
475 compared to undug sites in Figure 3 and 4 would suggest greater variability and  
476 heterogeneity of the community in undug locations. This is also supported by the  
477 IMD scores which also show a small reduction in variability and heterogeneity in dug  
478 areas and significantly lower variability as measured by PERMDISP for Fareham Creek  
479 and both sites combined. In fact,  $\beta$  diversity (variation) (see Anderson et al. [2011b]  
480 for definitions), as measured by a Bray Curtis resemblance matrix on  
481 presence/absence data, is also significantly lower for Dell Quay and when both sites  
482 are combined. These differences in community structure and  $\beta$  diversity between  
483 patches of dug and undug sediment will lead to an overall increase in  $\beta$  diversity at  
484 the site level (at least at Dell Quay). Recovery rates and size of any disturbance  
485 effect have been suggested to relate to the area of that disturbance (Munari et al.,  
486 2006; Carvalho et al., 2013). Frequently exploited sediment is, therefore, likely to  
487 show a much slower recovery period, thus ensuring differences persist and are  
488 exacerbated between patches. With this subsequent increase in site biodiversity  
489 (i.e. measured at larger spatial scales) our acceptance of the first hypothesis could be  
490 seen as positive. If changes in species, communities or biotopes are usually  
491 interpreted as compromising the integrity of the designated site (English Nature,  
492 2001), broad-scale increases in site biodiversity would be a considerable conundrum  
493 for conservation managers required to maintain inter-tidal mudflats in a favourable  
494 condition.

495

#### 496 4.4. Bird disturbance

497 The significant negative correlation for Dell Quay camera 1 between numbers of  
498 waders and numbers of bait collectors supports other work that waders are more  
499 sensitive to anthropogenic disturbance (Cardoni et al., 2008). Specifically, *Numenius*  
500 spp., *T. totanus* and *Haematopus* spp. are known to postpone their arrival into a

501 feeding site when humans are present (Fitzpatrick and Bouchez, 1998). It is likely  
502 that the increased vulnerability of these species is connected to their larger body  
503 mass (Liley et al., 2010). Larger birds rely less on crypsis and are, therefore, more  
504 alert resulting in a quicker flight response (Blumstein et al., 2005). The significant  
505 negative correlation with gulls was unexpected as they are disturbance-tolerant  
506 often returning first after an event (Smit and Visser, 1993). It has also been  
507 documented that gulls are attracted to spoil that is left behind from collection  
508 activity (James et al. unpubl, cited in Huggett, 1995). The response by gulls at Dell  
509 Quay may reflect a lack of anthropogenic habituation; or it may be possible that they  
510 have access to alternate feeding grounds when faced with potential disturbances  
511 and, therefore, fly away more readily (Gill et al. 2001). Liley and Fearnley (2012)  
512 found that the group least likely to respond to disturbance were wildfowl, such as  
513 mute swans (*Cygnus alor*) and this was the case here. Many of these species are fed  
514 by humans and personal observations have shown birds directly approach collectors.  
515 The lack of any significant negative relationships at Fareham Creek may be due to it  
516 being a highly disturbed site (a major road runs parallel to the creek and there are  
517 many people walking close by). It may be that the birds are habituated to the  
518 presence of collectors and people in general as this has been shown to occur for  
519 regular or constant noise (Smit and Visser, 1993).

520 The data presented here show that waders and gulls at Dell Quay move away from  
521 areas when collectors are present inducing a 'temporary loss of habitat' (Beale,  
522 2007) and supporting hypothesis two (at least for these groups and for this site). In  
523 fact, most of the relationships in Table 5 are negative indicating that generally fewer  
524 birds utilise the sites when collectors are on the shore. Any loss of habitat could be  
525 potentially detrimental to the birds' survival (Davidson and Rothwell, 1993). At the  
526 most simplistic level this loss of habitat equates to the area used by the collectors, so  
527 the frequency and duration of use by collectors means that a considerable area of  
528 inter-tidal mudflat may be routinely unavailable to birds at both sites.

529 The physiological consequences of disturbance need to be investigated and this  
530 could be with individual-based models. This has recently been attempted by  
531 Stillman et al. (2012) who showed that removing bait collection from a simulation

532 did not significantly increase the survival of waders. However, the authors  
533 acknowledged that this was because bait collection was classed as a relatively scarce  
534 activity (Liley et al., 2010). Our data and Watson et al. (2015) show that this is not  
535 the case and that the simulations need to be re-run using a model that is site-specific  
536 and has appropriate levels of bait collection.

537

#### 538 *4.5. Bait collection and management*

539 The benthic community plays a critical role in inter-tidal sediments with bioturbators  
540 such as polychaetes having an important influence on ecosystem function and  
541 services such as the cycling of nitrogen (Welsh, 2003). Whilst we have shown that  
542 collection for *A. virens* changes the sediment and macrofaunal community across  
543 large spatial scales, what is not clear is the impact on benthic function. If the  
544 essential function and services provided by the macrofaunal community regardless  
545 of the species composition remain unaffected, as has been reported for some  
546 offshore systems (e.g. Frid, 2010), then is there a requirement for direct  
547 management using MPAs and other systems? We recommend that prior to any  
548 implementation of bait collection management this question is investigated using a  
549 suite of functional approaches (Mouillot et al., 2013).

550 MPAs are often established under different conservation designations which include  
551 the protection of many wading bird species. Many of the invertebrate species  
552 recorded in this study are important prey items for this group (Prater, 1981).  
553 Reductions in the density of prey items reduce the food potential of the inter-tidal  
554 sediment; increasing foraging time and decreasing foraging success (Shepherd and  
555 Boates, 1999). A recent study by Bowgen et al. (2015) has confirmed that changes in  
556 prey density and size classes can produce dramatic changes in the modelled  
557 populations of wading birds. As bait collection occurs throughout the year (Watson  
558 et al., 2015), over such large spatial scales and in many other SPAs across the SEMS  
559 (Watson et al., 2007) these changes could be significant for multiple species of  
560 conservation importance. Changes in prey density;  $\beta$  diversity and site-specific  
561 responses due to bait collection should be included in any individual based model for

562 it to capture the link between direct (disturbance) and indirect (macrofaunal  
563 community) impacts.

564 Our data have shown that bait collection causes disturbance to some groups of birds,  
565 but it is just one of numerous disturbance-inducing activities (e.g. Ravenscroft et al.,  
566 2007; Liley and Fearnley, 2012) especially in multiuser MPAs. If management of bait  
567 collection within an MPA is to be based on bird disturbance alone then other similar  
568 disturbance-inducing activities must not be ignored.

569 Of critical importance for conservation legislation is whether the 'integrity' of the  
570 whole designated site is transformed. The integrity of the site has been defined as  
571 'the coherence of its ecological structure and function, across its whole area, that  
572 enables it to sustain the habitat, complex of habitats and/or the levels of populations  
573 of the species for which it was classified' (European Commission 2000). Broad-scale  
574 changes in species, communities or biotopes might be interpreted as compromising  
575 the integrity of the designated site, but some conservation agencies have concluded  
576 that even the loss of considerably less than 1% of designated sites could adversely  
577 affect site integrity (Hoskin and Tyldesley, 2006). However, as noted by Clark et al.,  
578 (2015) conservation efforts aimed at maintaining  $\alpha$  diversity may be less successful  
579 at preserving ecological integrity than efforts aimed at maintaining diversity of both  
580 species and communities at larger scales. Implementing local management methods  
581 without adequately assessing the impact at larger spatial scales could, therefore,  
582 result in unintentional changes at the hectare/site or regional scale. The increases in  
583  $\beta$  diversity driven by spatial heterogeneity between dug and undug areas could (if  
584 required) be promoted by appropriate management that would confine bait  
585 collection to specific sites within a region. We, therefore, recommend that  
586 management of biodiversity and function is at the most relevant scales for the  
587 habitat/species that are protected.

588 Bait collection is a globally valuable activity but also has significant impacts.  
589 Understanding the ecological impacts of bait fisheries will enable managers to better  
590 balance economic activity and conservation interventions such as MPAs in the  
591 framework of adaptive management. The challenge will be to provide the resources  
592 to collect data to understand the impacts of these fisheries at different spatial scales

593 and for different groups of protected species and habitats when budgets of  
594 conservation delivery organisations are already strained. This will be especially  
595 difficult in locations where it is just one of many activities within multi-user coastal  
596 MPAs that require management.

597

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605

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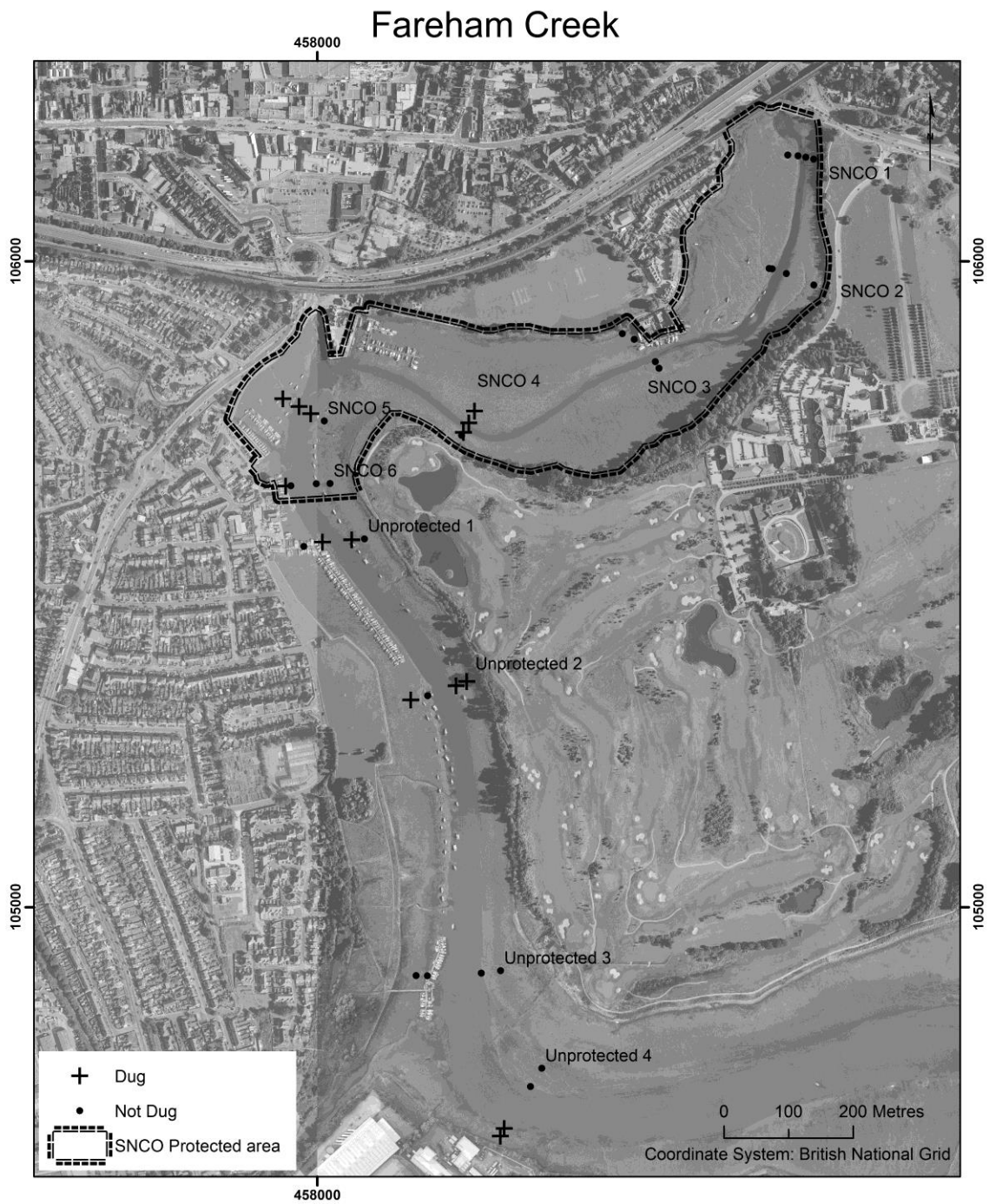
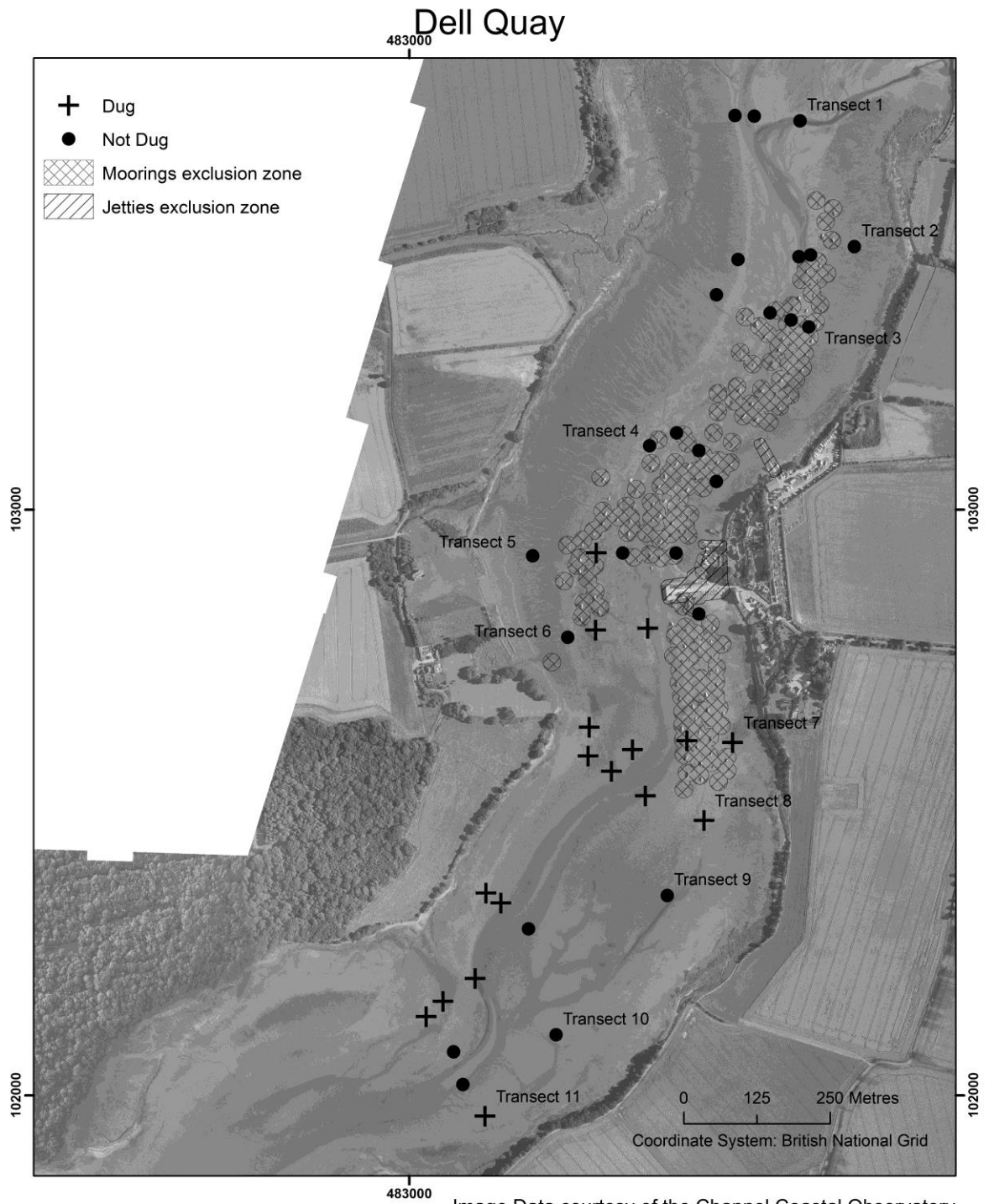


Image Data courtesy of the Channel Coastal Observatory  
<http://www.channelcoast.org/>

819

820 Figure S1. Map of Fareham Creek (Portsmouth Harbour) showing transect positions and sample  
821 locations with those cores located in dug areas denoted as crosses. Commercial bait collection is not  
822 permitted in the outlined area (within the SNCO).

823

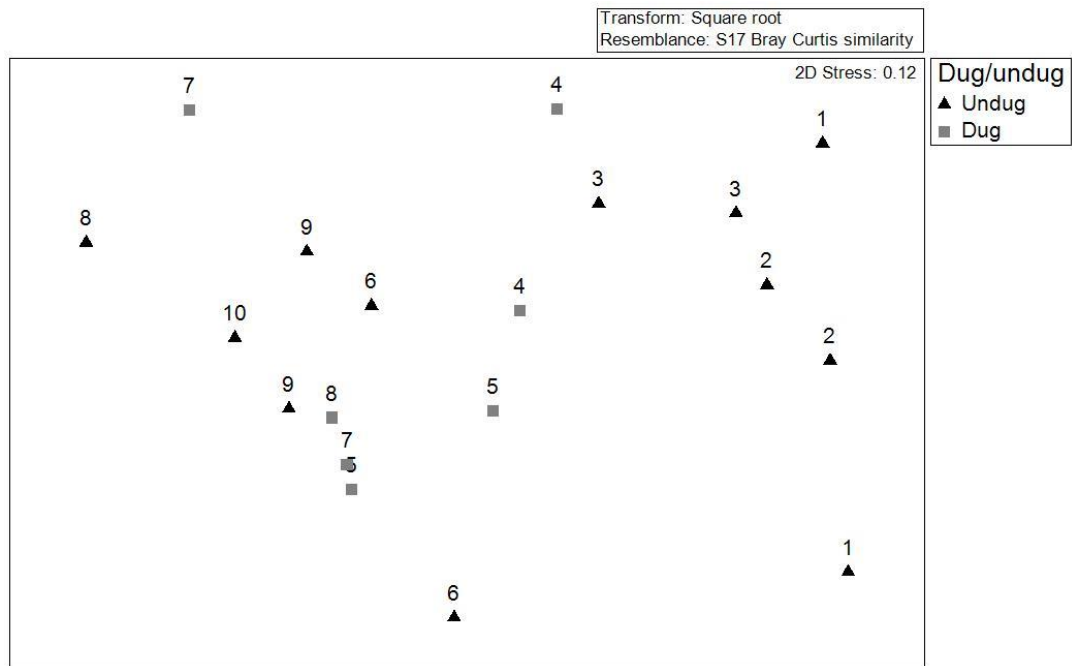


825

826 Figure S2. Map of Dell Quay (Chichester Harbour) showing transect positions and sample locations  
827 with those cores located in dug areas denoted as crosses. Exclusion zones for bait collection around  
828 moorings, quays and jetties are shown with cross hatching.

829

830 Figure 3

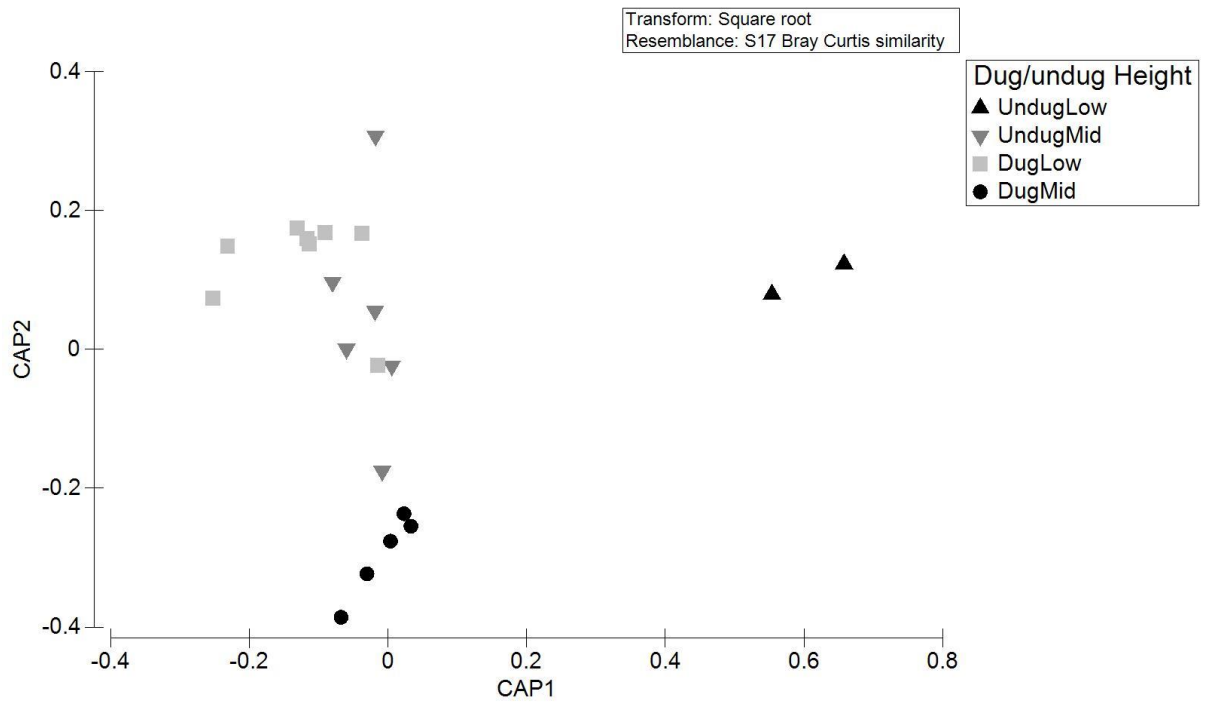


831

832 Figure 3. Plot of 2D-MDS for macrofauna community data on square root transformed Bray Curtis  
833 similarity matrix data of low shore cores from transects 1-6 (within protected) and 1-4 in unprotected  
834 area for Fareham Creek. Cores are grouped by transect and whether they were dug or undug.

835

836 Figure 4



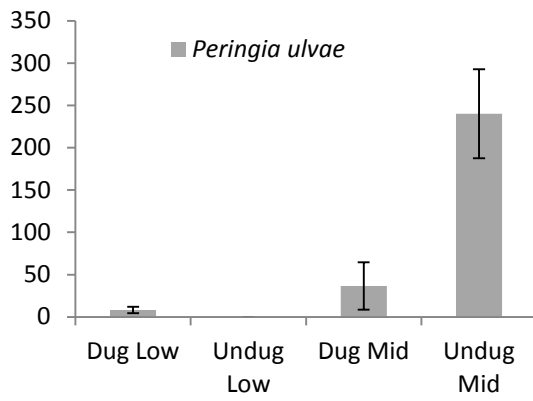
837

838 Figure 4. CAP plot for macrofauna community data of low and mid shore cores from transects from  
839 Dell Quay excluding protected cores. Cores are grouped by height on shore (low and mid) and  
840 whether they were dug or undug.

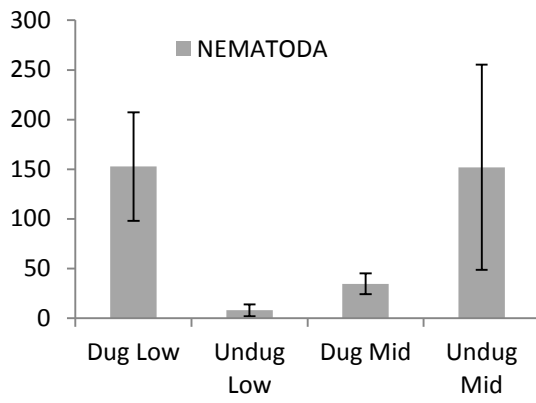
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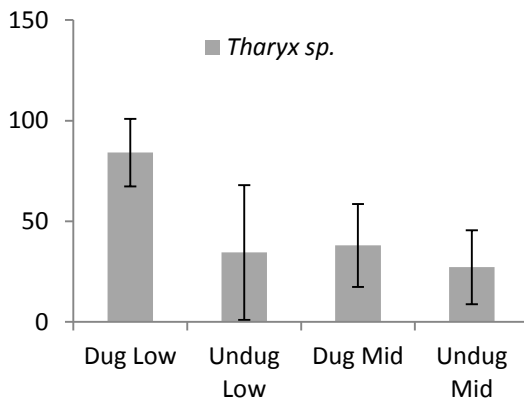
842 Figure 5



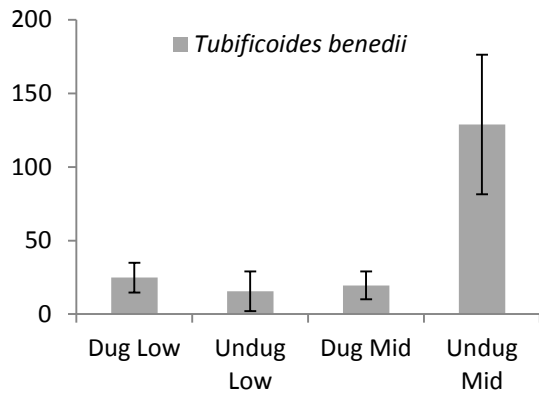
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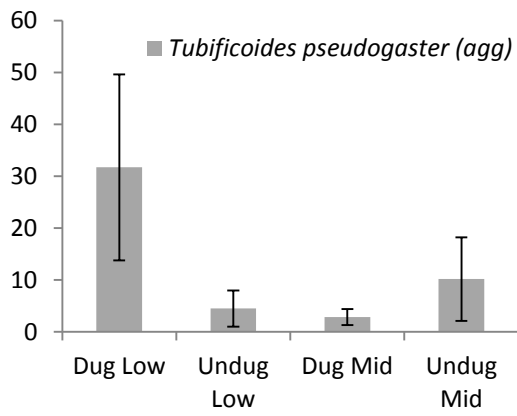
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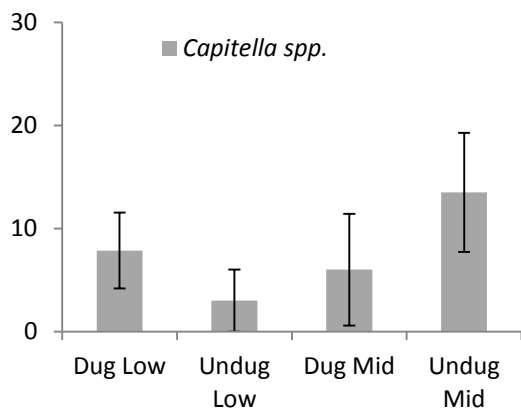
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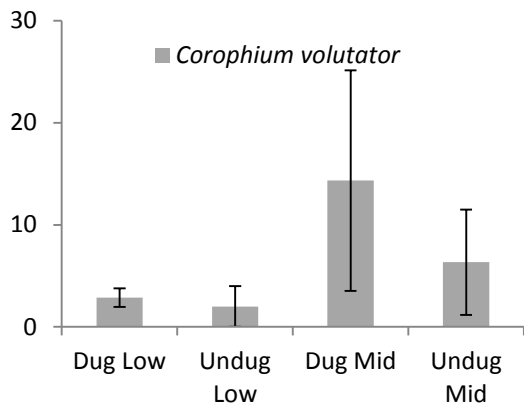
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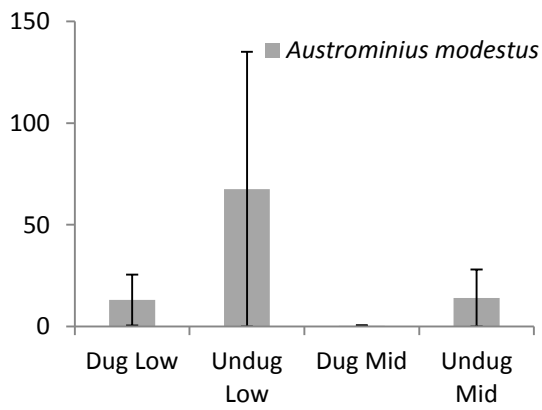
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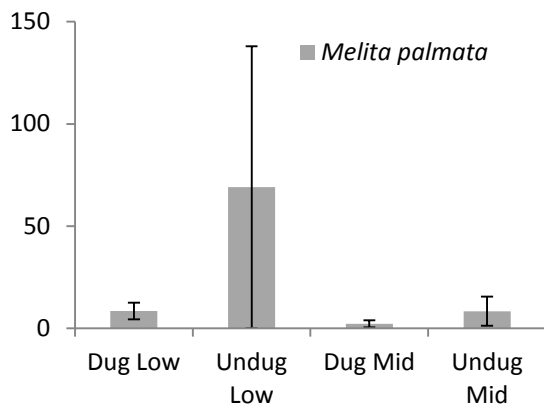
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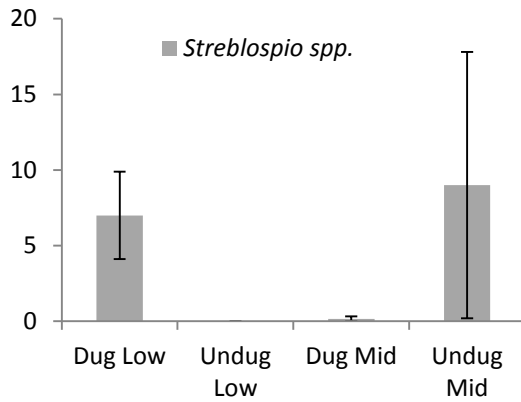
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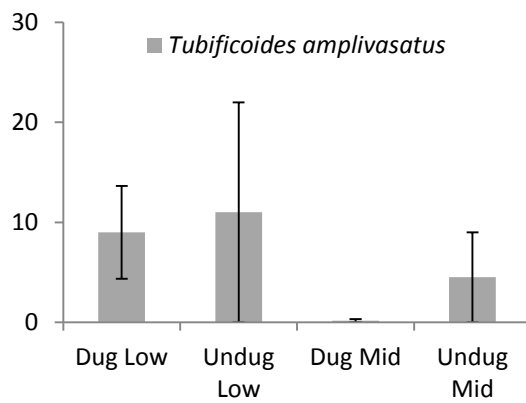
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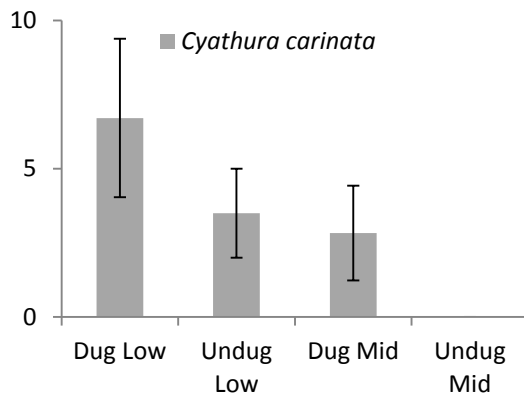
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855 Figure 5. Mean ( $\pm$ SEM) abundance per core for 12 most common species from low and mid shore  
 856 cores from transects from Dell Quay excluding cores from protected areas. Cores are grouped by  
 857 height on shore (low and mid) and whether they were dug or undug.

858

859 Table S1

Site	Dates	Camera location	Total area covered (m <sup>2</sup> )	Description
Dell Quay 1	2-16/3/12	South view 1	4501	Close to jetty west side of channel. Far edge of channel furthest boundary; nearest boundary cut across main channel and edge of jetty wall.
Dell Quay 3	17-28/2/12	South view 3	28306	South of jetty west side of channel. Far edge of channel furthest boundary: nearest boundary cut across main channel and edge of jetty wall.
Fareham Creek 1	1-8/11/12	Resident 1	3866	Golf course side of channel, upstream close to quay.
Fareham Creek 2	1-12/11/12	Resident 1	4633	Golf course side of channel, downstream of Camera 1, close to quay.

860

861 Table S1. Area (m<sup>2</sup>) of study sites recorded for each camera view for bird disturbance. The area of  
 862 mudflat covered by the camera (a trapezium due to view perspective) was measured on the ground  
 863 and total area back calculated.

864

865

<u>Fareham Creek</u>	Total n	Pro	n	Unpro	n	GLM test	Dug	n	Undug	n	GLM test	Low	n	Mid	n	GLM test
% Organic content	40	-	-	-	-	-	<b>3.82 ± 0.53</b>	<b>13</b>	<b>5.81 ± 0.60</b>	<b>27</b>	<b>F(1, 28) = 7.24, P=0.012</b>	4.31 ± 0.547	20	6.01 ± 0.705	20	F(1, 28) = 1.88, P=0.181
Mean diameter (µm)	39	-	-	-	-	-	286 ± 104	13	450 ± 130	26	F(1, 27) = 0.04, P=0.841	<b>535 ± 143</b>	<b>19</b>	<b>264 ± 117</b>	<b>20</b>	<b>F(1, 27) = 5.34, P=0.029</b>
% Mud	39	-	-	-	-	-	38.41 ± 3.28	13	39.41 ± 3.52	26	F(1, 27) = 0.08, P=0.777	34.77 ± 3.30	19	42.82 ± 3.77	20	F(1, 27) = 2.80, P=0.106
<u>Dell Quay</u>	Total n	Pro	n	Unpro	n	GLM test	Dug	n	Undug	n	GLM test	Low	n	Mid	n	GLM test
% Organic content	40	3.17 ± 0.60	13	2.86 ± 0.40	27	F(1, 26) = 2.79, P=0.107	<b>2.71 ± 0.35</b>	<b>16</b>	<b>3.49 ± 0.47</b>	<b>24</b>	<b>F(1, 26) = 19.58, P=0.000</b>	2.71 ± 0.41	22	3.27 ± 0.54	18	F(1, 26) = 0.00, P=0.957
Mean diameter (µm)	40	270 ± 71	13	473 ± 143	27	F(1, 39) = 0.08, P=0.787	614 ± 229	16	270 ± 57	24	F(1, 39) = 0.61, P=0.447	582 ± 167	22	194 ± 63.6	18	F(1, 39) = 1.73, P=0.211
% Mud	40	32.10 ± 4.31	13	34.54 ± 3.54	27	F(1, 39) = 2.72, P=0.123	26.9 ± 2.92	16	38.2 ± 3.91	24	F(1, 39) = 0.09, P=0.765	26.10 ± 2.07	22	43.08 ± 4.75	18	F(1, 26) = 25 P=0.623

866

867 Table 2. . Sediment particle size data (mean diameter [µm], % mud and % organic content) with ± standard error of mean for Dell Quay and Fareham Creek including  
868 details of GLM analysis of factors for Dell Quay (protected/unprotected; dug/undug; low/mid shore; transect) and Fareham Creek (dug/undug; low/mid shore; transect)  
869 with transect not shown for both sites. No interactions were included for Fareham Creek data. Interactions included for Dell Quay were as follows. Particle size:  
870 protected/unprotected and dug/undug; protected/unprotected and low/mid shore; low/mid shore and dug/undug; transect and low/mid shore. Percentage mud:  
871 protected/unprotected and dug/undug; protected/unprotected and low/mid shore; low/mid shore and dug/undug; transect and low/mid shore. All measures (except  
872 organic content) were calculated with the size of the <63 µm fraction specified at 1 µm and this was taken as being representative of the whole of this fraction. Bold  
873 indicates a significant difference between factors.

874

875

Fareham Creek	Total n	Pro	n	Unpro	n	GLM test	Dug	n	Undug	n	GLM test	Low	n	Mid	n	GLM test
S	19	-	-	-	-	-	15.00 ± 1.80	7	12.83 ± 1.22	12	F(1,8) = 3.18, P=0.112	-	-	-	-	-
n	19	-	-	-	-	-	559 ± 112	7	693 ± 220	12	F(1,8) = 1.22, P=0.301	-	-	-	-	-
Hill's N1	19	-	-	-	-	-	4.5 ± 0.57	7	3.8 ± 0.42	12	F(1,8) = 0.45 P=0.521	-	-	-	-	-
Dell Quay	Total n	Pro	n	Unpro	n	GLM test	Dug	n	Undug	n	GLM test	Low	n	Mid	n	GLM test
S	35	<b>11.27 ± 0.94</b>	<b>15</b>	<b>14.90 ± 1.45</b>	<b>20</b>	<b>F(1, 13) = 8.10, P=0.014</b>	14.53 ± 1.42	15	12.45 ± 1.30	20	F(1, 13) = 0.15, P=0.705	<b>15.22 ± 1.43</b>	<b>18</b>	<b>11.35 ± 1.13</b>	<b>17</b>	<b>F(1, 23) = 7.05, P=0.020</b>
n	35	410 ± 100	15	368 ± 60	20	F(1, 12) = 0.13, P=0.730	303 ± 59	15	449 ± 82	20	F(1, 12) = 0.33, P=0.575	348 ± 65	18	427 ± 89	17	F(1, 12) = 0.33, P=0.576
Hill's N1	35	<b>3.6 ± 0.34</b>	<b>15</b>	<b>5.3 ± 0.62</b>	<b>20</b>	<b>F(1, 12) = 12.4, P=0.004</b>	5.2 ± 0.65	15	4.1 ± 0.50	20	F(1, 12) = 0.00, P=0.953	5.3 ± 0.66	18	3.8 ± 0.40	17	F(1, 12) = 1.29, P=278

877

878 Table 3. Macrofauna sample diversity indices (Species number [S], numbers of individuals [n], Hill's N1 [N1] diversity index) with ± standard error of mean for Dell Quay and  
879 Fareham Creek including details of GLM analysis of factors: protected/unprotected; dug/undug; low/mid shore; transect for Dell Quay and dug/undug; transect for Fareham  
880 Creek with transect data not shown for both sites. Interactions that were included in each model for Dell Quay were as follows. Species number [S]: protected/unprotected and  
881 dug/undug; protected/unprotected and low/mid shore; and transect and low/mid shore. Number of individuals (n): protected/unprotected and dug/undug;  
882 protected/unprotected and low/mid shore; dug/undug and low/mid shore; and transect and low/mid shore. Hill's N1: protected/unprotected and dug/undug;

883 protected/unprotected and low/mid shore; dug/undug and low/mid shore; and transect and low/mid shore. All mid and low shore cores from transects 2- 10 from Dell Quay  
884 except Transect 10 were analysed, but only low shore cores were analysed for Fareham Creek.

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889



890 Table 4

	<b>IMD (Dug, undug compared)</b>	<b>Dispersion value (dug)</b>	<b>Dispersion value (undug)</b>
Fareham Creek	0.41	0.69	1.10
Dell Quay	0.33	0.92	1.24
<b>PERMDISP test</b>	<b>Significance test</b>	<b>Dug</b>	<b>Undug</b>
Fareham Creek	F(1, 17) = 6.72, P (perm) =0.027	32.7 (3.4)	41.4 (1.6)
Dell Quay	F(1, 33) = 1.29, P (perm) =0.335	37.2 (3.2)	43.2 (4.3)
Sites combined	F(1, 52) = 7.59, P (perm) =0.019	38.0 (2.0)	45.2 (1.6)
<b><math>\beta</math> diversity</b>	<b>Significance test</b>	<b>Dug</b>	<b>Undug</b>
Fareham Creek	F(1, 17) = 2.42, P (perm) =0.162	27.9 (2.2)	34.4 (2.4)
Dell Quay	F(1, 33) = 6.66, P (perm) =0.026	31.5 (2.8)	39.8 (1.9)
Sites combined	F(1, 52) = 8.93, P (perm) =0.01	32.2 (1.9)	39.4 (1.5)

891

892 Table 4. Dispersion values for dug and undug communities from each site and calculated Index of  
893 Multivariate Dispersion (IMD) scores. Higher dispersion values indicate greater variability and  
894 heterogeneity in a community and IMD values are calculated from the comparison between dug and  
895 undug areas. Homogeneity of dispersions between dug and undug communities for each site and  
896 combined is compared with square root transformation and Bray-Curtis similarity matrix using  
897 PERMDISP.  $\beta$  diversity (defined as variability in composition) for dug and undug communities for both  
898 sites and combined is calculated using PERMDISP on presence/absence data in conjunction with the  
899 Bray Curtis similarity matrix.

900

901 Table 5

Camera view	First variable	Second variable	Pearson's Product Moment Correlation	P-value
DQ Cam 1	Bait collectors	All birds	-0.1	0.267
DQ Cam 1	Bait collectors	Waders	<b>-0.197</b>	<b>0.027</b>
DQ Cam 1	Bait collectors	Gulls	-0.065	0.467
DQ Cam 1	Bait collectors	Wildfowl	0.093	0.3
DQ Cam 1	Bait collectors	Others	-0.072	0.422
DQ Cam 3	Bait collectors	All birds*	-0.035	0.733
DQ Cam 3	Bait collectors	Waders*	-0.1	0.334
DQ Cam 3	Bait collectors	Gulls*	<b>-0.211</b>	<b>0.04</b>
DQ Cam 3	Bait collectors	Wildfowl*	-0.068	0.510
DQ Cam 3	Bait collectors	Others*	0.041	0.693
FC Cam 2	Bait collectors	All birds*	-0.083	0.357
FC Cam 2	Bait collectors	Waders*	-0.098	0.274
FC Cam 2	Bait collectors	Gulls*	0.073	0.415
FC Cam 2	Bait collectors	Wildfowl*	0.009	0.920
FC Cam 2	Bait collectors	Others*	-0.090	0.318

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