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

Running head: the impacts of bait collection

G.J. Watson\textsuperscript{a*}, J. M. Murray\textsuperscript{b}, M. Schaefer\textsuperscript{c}, A. Bonner\textsuperscript{b}, M. Gillingham\textsuperscript{d}

\textsuperscript{a} Institute of Marine Sciences, School of Biological Sciences, University of Portsmouth, Ferry Road, Portsmouth, PO4 9LY, UK.
\textsuperscript{b} Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK.
\textsuperscript{c} Department of Geography, University of Portsmouth, Buckingham Building, Lion Terrace, Portsmouth, PO1 3HE
\textsuperscript{d} University of Portsmouth, Winston Churchill Avenue, Portsmouth, PO1 2UP, UK.

*Corresponding author

*Address: Institute of Marine Sciences, University of Portsmouth, Ferry Road, Portsmouth, PO4 9LY, UK. Telephone +44 (23) 92845798, E-mail: gordon.watson@port.ac.uk

Keywords: \textit{Alitta (Nereis) virens}, benthos, bait collection, birds, disturbance, fishery, Marine Protected Area, MPA

Word count: 8600 (excluding abstract and legends)
Abstract

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

Invertebrate species are increasingly exploited for human use with a dramatic rise in catch levels in recent decades (Anderson et al., 2011a), but not all are collected for food. Polychaete bait is an integral part of coastal life, but is perceived as a low value resource as fisheries are data-limited, locally focussed, and largely unregulated. However, a recent assessment has shown that the global catch is approximately 121,000 tonnes per annum with a retail value of £5.5 billion (Watson et al., 2017). This is comparable to many of the world’s most important fisheries, but in addition, productivities (i.e. biomass removed per m² of inter-tidal sediment) are orders of magnitude greater than many sub-tidal invertebrate fisheries (Watson et al., 2017).

In many locations ragworms are the major group collected from inter-tidal soft sediment shores with Alitta (Nereis) virens one of the most important species in Europe and the USA (Olive, 1994). For example, the UK fishery alone for this species is estimated to be 1500 t per annum (Watson et al., 2017). A. virens is a keystone inter-tidal species as prey for fish, birds and crustaceans; as a predator of other invertebrates and as an important bioturbator (McIntosh 1908-1910; Ambrose, 1986; Ambrose et al., 1998; Caron et al., 2004). Many studies have investigated the impacts of collecting a variety of bait species including lugworms (Blake, 1979; McLusky et al., 1983; van den Heiligenberg, 1987; Olive, 1993; Harvard and Tindal 1994; Beukema, 1995); bloodworms (Brown and Wilson, 1997; Ambrose et al., 1998; Beal and Vencile, 2001; Miller and Smith, 2012) and shrimps (Contessa and Bird, 2004; Skilleter et al., 2005; 2006; Winberg and Davis, 2014). Several have also investigated the impacts of sediment disturbance from other invertebrate inter-tidal fisheries (e.g. Beal and Vencile, 2001; Kaiser et al., 2001; Dernie et al., 2003; Logan, 2005; Griffiths et al., 2006; Masero et al., 2008; Navedo and Masero, 2008). Whilst all have shown impacts, the responses have been inconsistent; underlining the difficulty of extrapolating results across systems (e.g. different target species and source habitats). For those that have assessed ragworm collection (Blake, 1978; Olive, 1993; Brown and Wilson, 1997; Watson et al., 2007) and for many of the other studies, the relevant spatial scales (hectares) that bait collection covers have not
been used. Instead, small experimental plots have been established, but these suffer considerable artefacts such as macrofaunal migration from surrounding areas and that recovery rates and size of the effect are related to the area of disturbance (Munari et al., 2006; Carvalho et al., 2013). In addition, collection areas often correlate with spatial coverage of MPAs (Marine Protected Areas) used as a management tool in coastal areas (Wood et al., 2008). Surveys, therefore, assessing the impacts of ragworm collection on the macrofaunal community representative of the spatial scales (hectares) that bait collection covers are needed to support evidence-based management of these fisheries within MPAs.

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

In many locations bait collection remains a contentious issue for collectors, those organisations charged with minimising impact, and the associated coastal communities. Conservation legislation (e.g. European Union Natura 2000 sites) requires direct (Special Areas of Conservation [SACs]) and indirect (sub-features of Special Protection Areas [SPAs]) protection of inter-tidal mudflats to maintain them in favourable condition. In other words, subject to natural change, the range and distribution of characteristic biotopes and abundance of prey species for birds of interest must be maintained (English Nature, 2001). Overlap of protected coastal habitat and areas with high levels of collection gives great scope for conflict in many parts of the world. Effective management of bait collection in areas of protected inter-tidal mudflat (including areas protected for wading birds and wildfowl) requires
an understanding of these impacts. Using two popular UK collection sites within the
Solent region (part of the Solent European Marine Site [SEMS]) as case studies we
mapped the extent of dug areas and collected cores for macrofaunal and sediment
analysis from multiple transects located in dug/undug and low and mid shore areas
to test hypothesis one: 1. Collection of *A. virens* by digging will significantly alter the
macrofaunal community and the associated sediment characteristics over large (i.e.
MPA-relevant covering several hectares) spatial scales. Remote Closed Circuit
Television [CCTV] cameras were then used to record the numbers of collectors and
abundance and diversity of birds on the inter-tidal sediment to test hypothesis two:
2. The presence of collectors on the sediment will reduce the bird abundance of
waders and wildfowl utilising the same location.

2. Materials and Methods

2.1. Biotope surveys and sample collection

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

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

Bait dug areas were defined as those exhibiting characteristics based on our own observations and those of Coates (1983), Brown and Wilson (1997) and Fearnley et al. (2013). These included: uneven topography (the area has mounds, water-filled depressions and troughs); the presence of empty bivalve shells and stones on the surface; a lack of algal mat cover; and the presence of darker (anoxic) sediment on the surface. Turned over sediment can persist for variable lengths of time depending on the energy of the site (Coates, 1983; McLusky et al., 1983; Sypitkowski et al., 2010; Fearnley et al., 2013). It was not possible to directly record the ‘age’ of the dug sediment from which cores were taken as collectors were not individually tracked. However, monthly assessment (January-June 2016) of four replicate 1 m² dug areas in the Solent intertidal area confirms dug sediment persists for 83 ± 30 days SD in low energy shores. We, therefore, assumed that dug areas were dug a maximum of 12 weeks prior to sampling.

A systematic sampling strategy for macrofaunal and sediment analysis was performed with 10 transects at Fareham Creek (Figure S1) and 11 transects at Dell Quay (Figure S2) covering both nominally protected and unprotected areas. Four sampling stations (two mid-shore and two low-shore either side of the central channel) were located and at each one 0.01 m² (15 cm deep) core was taken and fixed in 10% formalin in seawater for faunal analysis. An additional 5 cm diameter core was taken at each station and frozen (-20°C) for future sediment analysis.

2.2. Sample processing

Sediment cores were heated at 60°C until completely dry and processed using wet sieving for particle size analysis and loss on ignition at 475°C for 4.5 hours for organic content (Buchanan, 1984). All cores (39 cores in total) from Fareham Creek and all except one from transect 7 (40 cores in total) for Dell Quay were analysed for sediment characteristics. Samples to be processed for macrofaunal analysis were chosen a posteriori according to the following scheme due to financial restrictions.
At Fareham Creek all cores from the low shore were processed except one unprotected from transect 4 due to its loss (19 cores in total). All cores (low and mid shore) for Dell Quay from transects 2 -10 except one from transect 10 were processed (35 cores in total) (see Figures S1 and S2).

2.3. CCTV installation and video analysis for bird disturbance

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

2.4. Data analysis

Macrofaunal species abundance data were synonymised with the WoRMS (2016) database before excluding terrestrial and planktonic species. Univariate and multivariate methods (e.g. non-metric multi-dimensional scaling ordination based on a square root transformed Bray Curtis similarity matrix of species abundance) followed by SIMPER, PERMANOVA and CAP (Canonical Analysis of Principal
Components) were used, where appropriate, for the macrofauna data using PRIMER v 6.0 (Anderson and Willis, 2003; Anderson et al., 2008). Multivariate dispersion between dug and undug communities was assessed using the Index of Multivariate Dispersion (IMD) and PERMDISP routines. According to Anderson et al. (2006) PERMDISP is directly interpretable as a test for similarity in β diversity (defined as variability in composition) among groups when used on presence/absence data in conjunction with the Bray Curtis similarity matrix. Data were, therefore, transformed to presence/absence and analysed with this routine.

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

Species number (S), number of individuals (n), Hill’s N1 diversity index and sediment characteristics were analysed further using General Linear Models (including, if appropriate, protected/unprotected, dug/undug, transect, low/mid shore as factors) and transformed to meet any parametric assumptions as required. This was achieved for all analyses except Hill’s N1 diversity index for Dell Quay as the variances could not be equalised. Models were run including interactions if the hierarchical structure of the data allowed. To achieve a simplified model, interactions were subsequently excluded if found not to be significant (Gardiner, 1997; Crawley, 2007) and then the reduced and full models were compared using the adjusted deviance R² to select the one with the best fit. Analysis of individual species abundances for Dell Quay were attempted with a variety of GLM (with transformation), Poisson and other regression models, but none provided an appropriate fit for the data. Consequently, only graphical presentations were employed to show these data. Correlations for bird abundance and bait collector activity were performed using a Pearson Correlation with the first seven days of data per site/view analysed to standardise the number of days between camera runs.
3. Results

3.1. The effects of bait collection on sediment

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

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

Principal sediment description types for Dell Quay were also fine sands with an associated overall site mean particle size of 407 ±99 µm. Sediment particles were very poorly sorted, symmetrical in terms of skewness and very platykurtic for kurtosis. The mean percentage level of mud and organic content were 33.7 ± 2.7 % and 2.96 ±0.3%, respectively. Variability between cores for all measurements was still present, but less so than at Fareham Creek.

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

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

3.2. Macrofaunal diversity

**Fareham Creek**

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

**Dell Quay**
Four taxa (nematodes, \textit{Tharyx} sp., \textit{P. ulvae} and \textit{T. benedii}) accounted for 75\% of the total number of individuals recorded with one of these species accounting for up to 90\% in some cores. Univariate analyses of species abundance mainly showed no significant differences between the factors when analysed with General Linear Models except for Hill’s N1 and S (Table 3). For S, cores from protected areas and the mid shore had significantly higher numbers of species (approximately four more species on average per core) with significant differences also between transects ($F = 3.58, \ p = 0.020$). There were also significant interaction terms (protected/unprotected and dug/undug [$F = 7.33, \ p = 0.018$]; protected/unprotected and height [$F = 10.9, \ p = 0.006$]; and height and transect [$F = 4.1, \ p = 0.013$]).

Diversity (Hill’s N1) was significantly higher in unprotected areas and there were also significant interaction terms (protected/unprotected and dug/undug [$F = 6.7, \ p = 0.023$]; protected/unprotected and height [$F = 24.6, \ p > 0.001$]; and height and transect [$F = 3.9, \ p = 0.017$]). Analysis using PERMANOVA with all factors (protected/unprotected, dug/undug, transect and height on shore) shows that significant community differences were present for all factors (protected/unprotected, pseudo $F = 2.94, \ p = 0.013$; dug/undug, pseudo $F = 4.12, \ p = 0.006$; transect, pseudo $F = 1.87, \ p = 0.015$; and height on shore, pseudo $F = 2.96, \ p = 0.024$) in addition to a significant interaction for transect and height on shore ($F = 1.81, \ p = 0.037$). Changes in the relative dispersion of the community (IMD) between dug and undug cores confirmed greater variability in species compositional structure in undug locations. These changes were not significant when analysed using PERMDISP for Dell Quay alone, but were when the sites were combined (Table 4).

No significant differences between protected and unprotected, and shore height were present as measured by PERMDISP (data not shown). Significant differences in $\beta$ diversity between dug and undug cores were also seen for Dell Quay and when both sites were combined.

It is important for the interrogation of digging effects to first reduce the influence of protection. To facilitate further analysis all cores collected from protected areas were excluded and the remaining data reanalysed with CAP. Figure 4 confirms that the canonical axes separate the dug from the undug sites, but also those from low
and mid shore. This clearly shows an impact of digging on the macrofaunal community, but also height on shore was important in determining the community response (the importance of both variables is confirmed by the permutation trace statistic of 2.42, p = 0.001). SIMPER analysis was used to investigate which species contribute most to the dissimilarity between dug and undug cores. Average dissimilarity was 64.9, but the difference is again with contributions from a large number of species. For example, five of the most abundant species contributed only 52% of the dissimilarity. To explore which species might be important the mean abundance for the 12 most common species from these cores are plotted split between: dug, undug, low and mid shore (Figure 5). Although there were some notable exceptions e.g. Tharyx sp., Cyathura carinata and Corophium volutator, the mid shore dug cores had consistently lower abundances than their undug counterparts. However, for the dug low shore cores only half the species had lower or similar abundances to undug cores (P. ulvae, T. benedii, Capitella spp., C. volutator, Melita palmata, Austrominius modestus, and T. amplivatus).

3.3. Disturbance to birds

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

4.1 Bait collection at the sites

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

4.2. Effects of protection and shore height

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

All univariate measures except n (total number of individuals) were higher in the low shore area for Dell Quay, although only differences in the number of recorded taxa (S) were statistically significant. Differences in community structure between shore heights are not surprising considering benthic invertebrate biomass changes with emersion time (e.g. Beukema, 1976; Griffiths et al., 2006). It is likely that the different sediment characteristics between low and mid shore areas at Dell Quay are, in combination with physical variables that vary with shore height, responsible for the differences in community structure.
At Dell Quay the exclusion zones round moorings and jetties were successful in preventing collection, but resulted in increases in numbers of species (S) and diversity (Hill’s N1 index) in addition to a change in the macrofaunal community (as measured by PERMANOVA). As other influences are confounded with protection further work is required to understand the interaction of the different processes. Scouring of the sediment by buoy-attachment chains reduces the median sediment particle size and changes the macrofaunal community and abundance of certain species (Herbert et al., 2009). As the majority of cores within protected areas came from areas close to boat moorings rather than jetties, scouring is likely to be responsible for the effects of protection. It is, therefore, important to consider the integration of bait exploitation management with management of existing site-specific activities (e.g. recreational boating) to ensure that they are additive in their effects.

4.3. Effects of bait collection

Data presented here show for the first time that changes occur in the sediment and macrofaunal communities over large spatial scales when ragworms are collected for bait. Significant differences between dug and undug sediment were restricted to organic content, and for Dell Quay mean particle size was also lower in undug areas, although not significantly so. Together these show that undug sediment was muddier with a higher organic content and, in contrast to Carvalho et al. (2013), the response is generally not site-specific. Turning over the sediment changes the microtopography leading to the loss of the finer fractions and associated organic material as it is washed away by tides and wave action. This is likely to have important implications for local sediment load and turbidity levels. In addition, as organic matter binds many contaminants (Eggleton and Thomas, 2004) and sediment disturbance leads to desorption of pollutants (Edge et al., 2015), an increase in bioavailability from bait collection is highly likely as shown by Howell (1985) for cadmium. The impacts of collection may, therefore, go well beyond the extent of dug sediment.
The distribution of benthic assemblages is known to relate to sediment characteristics (Snelgrove and Butman, 1994), but the responses to bait collection were site specific. At Fareham Creek the sediment changes observed did not result in significant changes to the macrofaunal community, although a significant increase in variability was recorded for dispersion. The significant differences in community structure between transects indicate the presence of a gradient down the creek (likely to be related to the freshwater input) and could have masked any digging-induced changes. Transect differences may also have been responsible for the reduction in variability for dug sites, but the number of replicates per transect precluded an analysis for this factor. Contrary to the influence of location (i.e. freshwater input) at Fareham Creek, the gradient at Dell Quay did not mask the changes seen at that site measured by PERMANOVA. In contrast to Fareham Creek, collectors at Dell Quay spent the majority of their time digging in areas that had already been dug (Watson et al., 2015). The cumulative impacts of repeated digging such as preventing recovery of small macrofauna species (Brown and Wilson, 1997) may have been sufficient for the differences to manifest themselves in the sediment and through to the macrofaunal community at Dell Quay.

According to Clarke and Gorley (2006) diversity indices are unable to detect subtle changes in a complex community and this is supported by the general lack of significant differences in GLMs for the univariate measures. In contrast, multivariate analyses show for the first time that ‘natural levels’ of hand-collection for *A. virens* produce significant changes in the macrofaunal community evident over large (hectares) spatial scales, in addition to responding to environmental factors such as shore height and location within the site (transect position). Responses of benthic species to disturbance often vary (e.g. McLusky et al., 1983; Harvard and Tindal, 1994; Whomersley et al., 2010; Carvalho et al., 2013) and this was the case here. Increases in the abundance of *Tharyx* sp., *C. carinata* and *C. volutator* in dug areas on the mid shore and nematodes, *Tharyx* sp., *T. pseudogaster*, *Capitella* spp., *Streblospio* spp. and *C. carinata* on the low shore contrast with large reductions in *P. ulvae*, nematodes and *T. benedii* for the mid shore and smaller reductions for *M. palmata* and *E. modestus* for the low shore areas (Figure 5). Brown and Wilson...
(1997) and Masero et al. (2008) suggested that small surface-dwelling species are sensitive to disturbance, and Whormersley et al. (2010) showed that different disturbance types and intensities could change the trophic group ratios within a community. However, even these more broad-scale responses were still site and disturbance type specific. Our data also show that responses were not consistent between species (e.g. C. volutator and P. ulvae) or even between those within the same trophic group (e.g. T. benedii and T. pseudogaster as sub-surface deposit feeders; C. volutator and Streblospio spp. as surface deposit feeders). One explanation for this inconsistency is that, although we classified all dug sediment as being dug within 12 weeks of sampling, small species may recover in this timeframe leading to an increase in heterogeneity. Increased heterogeneity related to stress has been shown to occur for macrobenthos and other communities (Warwick and Clarke, 1993), although this is not supported by the IMD values or the PERMDISP analyses as both show a reduction in community variability in areas that are dug. Future work should include a method of assessing the age of dug sediment, however, the fact that differences between dug and undug sediment were present despite any partial recovery would suggest an even stronger response if dug sediment of the same age was compared. Our data, therefore, support our first hypothesis that collection alters the macrofaunal community and the associated sediment characteristics across large spatial scales, but with the caveat that the strength (and type) of the response is site specific. This is corroborated by data from Whomersley et al. (2010) who suggested that sites respond differently, not simply because of differences in species or trophic group, but because of inherent ecological plasticity exhibited by many benthic species (Davic, 2003) combined with history of prior disturbance.

Bait collection adds another layer of variation to already spatially diverse inter-tidal benthic systems where communities are influenced by site, height on shore and the presence of built structures as well as many other anthropogenic effects. Bait collection at these sites, and more generally, is temporally variable (Fowler, 2001; Sypitkowski et al., 2010; Miller and Smith, 2012; Watson et al., 2015). Combined with the spatial variability (patchiness) recorded here, sites where bait collection
occurs could be described as already heterogeneous areas overlaid with intermittently repeating disturbance at different spatial and temporal scales. In the context of the Intermediate Disturbance Hypothesis (Grime, 1973; Connell, 1978) this patchiness might lead to an overall increase in $\beta$ diversity at the hectare/site scale. Inspection of the dispersion of the community data of cores from dug sites compared to undug sites in Figure 3 and 4 would suggest greater variability and heterogeneity of the community in undug locations. This is also supported by the IMD scores which also show a small reduction in variability and heterogeneity in dug areas and significantly lower variability as measured by PERMDISP for Fareham Creek and both sites combined. In fact, $\beta$ diversity (variation) (see Anderson et al. [2011b] for definitions), as measured by a Bray Curtis resemblance matrix on presence/absence data, is also significantly lower for Dell Quay and when both sites are combined. These differences in community structure and $\beta$ diversity between patches of dug and undug sediment will lead to an overall increase in $\beta$ diversity at the site level (at least at Dell Quay). Recovery rates and size of any disturbance effect have been suggested to relate to the area of that disturbance (Munari et al., 2006; Carvalho et al., 2013). Frequently exploited sediment is, therefore, likely to show a much slower recovery period, thus ensuring differences persist and are exacerbated between patches. With this subsequent increase in site biodiversity (i.e. measured at larger spatial scales) our acceptance of the first hypothesis could be seen as positive. If changes in species, communities or biotopes are usually interpreted as compromising the integrity of the designated site (English Nature, 2001), broad-scale increases in site biodiversity would be a considerable conundrum for conservation managers required to maintain inter-tidal mudflats in a favourable condition.

4.4. Bird disturbance

The significant negative correlation for Dell Quay camera 1 between numbers of waders and numbers of bait collectors supports other work that waders are more sensitive to anthropogenic disturbance (Cardoni et al., 2008). Specifically, *Numenius* spp., *T. totanus* and *Haematopus* spp. are known to postpone their arrival into a
feeding site when humans are present (Fitzpatrick and Bouchez, 1998). It is likely that the increased vulnerability of these species is connected to their larger body mass (Liley et al., 2010). Larger birds rely less on crypsis and are, therefore, more alert resulting in a quicker flight response (Blumstein et al., 2005). The significant negative correlation with gulls was unexpected as they are disturbance-tolerant often returning first after an event (Smit and Visser, 1993). It has also been documented that gulls are attracted to spoil that is left behind from collection activity (James et al. unpubl, cited in Huggett, 1995). The response by gulls at Dell Quay may reflect a lack of anthropogenic habituation; or it may be possible that they have access to alternate feeding grounds when faced with potential disturbances and, therefore, fly away more readily (Gill et al. 2001). Liley and Fearnley (2012) found that the group least likely to respond to disturbance were wildfowl, such as mute swans (Cygnus alor) and this was the case here. Many of these species are fed by humans and personal observations have shown birds directly approach collectors. The lack of any significant negative relationships at Fareham Creek may be due to it being a highly disturbed site (a major road runs parallel to the creek and there are many people walking close by). It may be that the birds are habituated to the presence of collectors and people in general as this has been shown to occur for regular or constant noise (Smit and Visser, 1993).

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

The physiological consequences of disturbance need to be investigated and this could be with individual-based models. This has recently been attempted by Stillman et al. (2012) who showed that removing bait collection from a simulation
did not significantly increase the survival of waders. However, the authors acknowledged that this was because bait collection was classed as a relatively scarce activity (Liley et al., 2010). Our data and Watson et al. (2015) show that this is not the case and that the simulations need to be re-run using a model that is site-specific and has appropriate levels of bait collection.

4.5. Bait collection and management

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

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

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

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

Bait collection is a globally valuable activity but also has significant impacts. Understanding the ecological impacts of bait fisheries will enable managers to better balance economic activity and conservation interventions such as MPAs in the framework of adaptive management. The challenge will be to provide the resources to collect data to understand the impacts of these fisheries at different spatial scales.
and for different groups of protected species and habitats when budgets of conservation delivery organisations are already strained. This will be especially difficult in locations where it is just one of many activities within multi-user coastal MPAs that require management.

5. Acknowledgements

The authors acknowledge the financial support of the Crown Estate and Natural England. The authors would also like to thank the staff and students of the Institute of Marine Sciences for sample collection, processing and analysis. Additional thanks to staff of EMU Ltd, G. James, R. Carver, E. Rowsell, G. Horton, H. Pardo, R. Williams, F. Wynne and the Solent Forum for assistance, comments and guidance. Finally, thanks to T. Willis for PRIMER assistance and S. Bolam for manuscript comments.

6. References


Beal BF, Vencile KW (2001) Short-term effects of commercial clam (Mya arenaria L.) and worm (Glycera dibranchiate Ehlers) harvesting on survival and growth of juveniles of the soft-shell clam. J Shellfish Res 20: 1145-1157


Bowgen KM, Stillman RA, Herbert RJH (2015) Predicting the effect of invertebrate regime shifts on wading birds: insights from Poole Harbour, UK. Biol Cons 186: 60-68


Coates PJ (1983) Fishing bait collection in the Menai Strait and its relevance to the potential establishment of a Marine Nature Reserve with observations of the biology of the main prey species, the ragworm *Nereis virens*. MSc Imperial College, University of London.


definition of the keystone concept. Conser Ecol 7: r11

Davidson NC, Rothwell PI (1993) Disturbance to waterfowl on estuaries: the
conservation and coastal management implications of current knowledge. Wader
Study Group Bull 68: 97-105

following physical disturbance J App Ecol 72: 1043-1056

Edge KL, Dafforn KA, Simpson SL, Roach AC, Johnson EL (2015) A biomarker of
contaminant exposure is effective in large scale assessment of ten estuaries.
Chemosphere 100: 16-26

Eggleton J, Thomas KV (2004) A review of factors affecting the release and
bioavailability of contaminants during sediment disturbance events. Environ Int
30: 973-980

Solent European marine site given under Regulation 33(2) of the Conservation
(Natural Habitats) Regulations 1994, pp 117

6 of the 'Habitats' Directive 92/43/EEC. Brussels

Bird Distribution and Foraging Behaviour in Poole Harbour SPA. Report for Natural

behaviour of waders on a rocky beach. Bird Study 45: 157-171

Folk RL, Ward WC (1957) Brazos River bar: a study in the significance of grain size
parameters. J Sedimentary Petrology 27: 3-26

Fowler SL (2001) Investigation into the extent of bait collection and its impacts on
features of conservation interest for birds and intertidal species and habitats
within the Solent Natural Area. Report for English Nature pp 102


Hoskin R, Tyldesley D (2006) How the scale of effects on internationally designated nature conservation sites in Britain has been considered in decision making: A review of authoritative decisions. English Nature Research Reports, No. 704


McIntosh WC (1908-1910) British marine annelids, vol. 2. London, Ray Society


Watson GJ, Murray JM, Schaefer M, Bonner A (2017) Bait worms: a valuable and important fishery with implications for fisheries and conservation management. Fish and Fisheries (accepted), DOI: 10.1111/faf.12178


Figure S1. Map of Fareham Creek (Portsmouth Harbour) showing transect positions and sample locations with those cores located in dug areas denoted as crosses. Commercial bait collection is not permitted in the outlined area (within the SNCO).
Figure S2. Map of Dell Quay (Chichester Harbour) showing transect positions and sample locations with those cores located in dug areas denoted as crosses. Exclusion zones for bait collection around moorings, quays and jetties are shown with cross hatching.
Figure 3. Plot of 2D-MDS for macrofauna community data on square root transformed Bray Curtis similarity matrix data of low shore cores from transects 1-6 (within protected) and 1-4 in unprotected area for Fareham Creek. Cores are grouped by transect and whether they were dug or undug.
Figure 4. CAP plot for macrofauna community data of low and mid shore cores from transects from Dell Quay excluding protected cores. Cores are grouped by height on shore (low and mid) and whether they were dug or undug.
Figure 5

- **Peringia ulvae**
  - Dug Low
  - Undug Low
  - Dug Mid
  - Undug Mid

- **NEMATODA**
  - Dug Low
  - Undug Low
  - Dug Mid
  - Undug Mid

- **Tharyx sp.**
  - Dug Low
  - Undug Low
  - Dug Mid
  - Undug Mid
Figure 5. Mean (±SEM) abundance per core for 12 most common species from low and mid shore cores from transects from Dell Quay excluding cores from protected areas. Cores are grouped by height on shore (low and mid) and whether they were dug or undug.
<table>
<thead>
<tr>
<th>Site</th>
<th>Dates</th>
<th>Camera</th>
<th>Total area covered (m²)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dell Quay 1</td>
<td>2-16/3/12</td>
<td>South</td>
<td>4501</td>
<td>Close to jetty west side of channel. Far edge of channel furthest boundary; nearest boundary cut across main channel and edge of jetty wall.</td>
</tr>
<tr>
<td>Dell Quay 3</td>
<td>17-28/2/12</td>
<td>South</td>
<td>28306</td>
<td>South of jetty west side of channel. Far edge of channel furthest boundary: nearest boundary cut across main channel and edge of jetty wall.</td>
</tr>
<tr>
<td>Fareham Creek 1</td>
<td>1-8/11/12</td>
<td>Resident</td>
<td>3866</td>
<td>Golf course side of channel, upstream close to quay.</td>
</tr>
<tr>
<td>Fareham Creek 2</td>
<td>1-12/11/12</td>
<td>Resident</td>
<td>4633</td>
<td>Golf course side of channel, downstream of Camera 1, close to quay.</td>
</tr>
</tbody>
</table>

Table S1. Area (m²) of study sites recorded for each camera view for bird disturbance. The area of mudflat covered by the camera (a trapezium due to view perspective) was measured on the ground and total area back calculated.
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 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) 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: protected/unprotected and dug/undug; protected/unprotected and low/mid shore; low/mid shore and dug/undug; transect and low/mid shore. Percentage mud: 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 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 indicates a significant difference between factors.

<table>
<thead>
<tr>
<th>Fareham Creek</th>
<th>Total n</th>
<th>Pro n</th>
<th>Unpro n</th>
<th>GLM test</th>
<th>Dug n</th>
<th>Undug n</th>
<th>GLM test</th>
<th>Low n</th>
<th>Mid n</th>
<th>GLM test</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Organic content</td>
<td>40</td>
<td>-</td>
<td>-</td>
<td></td>
<td>3.82 ± 0.53</td>
<td>13</td>
<td>5.81 ± 0.60</td>
<td>27</td>
<td>F(1, 28) = 7.24, P=0.012</td>
<td>4.31 ± 0.547</td>
</tr>
<tr>
<td>Mean diameter (µm)</td>
<td>39</td>
<td>-</td>
<td>-</td>
<td></td>
<td>286 ± 104</td>
<td>13</td>
<td>450 ± 130</td>
<td>26</td>
<td>F(1, 27) = 0.04, P=0.841</td>
<td>535 ± 143</td>
</tr>
<tr>
<td>% Mud</td>
<td>39</td>
<td>-</td>
<td>-</td>
<td></td>
<td>38.41 ± 3.28</td>
<td>13</td>
<td>39.41 ± 3.52</td>
<td>26</td>
<td>F(1, 27) = 0.08, P=0.777</td>
<td>34.77 ± 3.30</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Dell Quay</th>
<th>Total n</th>
<th>Pro n</th>
<th>Unpro n</th>
<th>GLM test</th>
<th>Dug n</th>
<th>Undug n</th>
<th>GLM test</th>
<th>Low n</th>
<th>Mid n</th>
<th>GLM test</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Organic content</td>
<td>40</td>
<td>3.17 ± 0.60</td>
<td>13</td>
<td>2.86 ± 0.40</td>
<td></td>
<td>2.71 ± 0.35</td>
<td>16</td>
<td>3.49 ± 0.47</td>
<td>24</td>
<td>F(1, 26) = 19.58, P=0.000</td>
</tr>
<tr>
<td>Mean diameter (µm)</td>
<td>40</td>
<td>270 ± 71</td>
<td>13</td>
<td>473 ± 143</td>
<td></td>
<td>614 ± 229</td>
<td>16</td>
<td>270 ± 57</td>
<td>24</td>
<td>F(1, 39) = 0.61, P=0.447</td>
</tr>
<tr>
<td>% Mud</td>
<td>40</td>
<td>32.10 ± 4.31</td>
<td>13</td>
<td>34.54 ± 3.54</td>
<td></td>
<td>26.9 ± 2.92</td>
<td>16</td>
<td>38.2 ± 3.91</td>
<td>24</td>
<td>F(1, 39) = 0.09, P=0.765</td>
</tr>
</tbody>
</table>
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 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 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 dug/undug; protected/unprotected and low/mid shore; and transect and low/mid shore. Number of individuals (n): protected/unprotected and dug/undug; 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;

<table>
<thead>
<tr>
<th>Fareham Creek</th>
<th>Total n</th>
<th>Pro n</th>
<th>Unpro n</th>
<th>GLM test</th>
<th>Dug n</th>
<th>Undug n</th>
<th>GLM test</th>
<th>Low n</th>
<th>Mid n</th>
<th>GLM test</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>19</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>15.00 ± 1.80</td>
<td>7</td>
<td>12.83 ± 1.22</td>
<td>12</td>
<td>F(1,8) = 3.18, P=0.112</td>
</tr>
<tr>
<td>n</td>
<td>19</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>559 ± 112</td>
<td>7</td>
<td>693± 220</td>
<td>12</td>
<td>F(1,8) = 1.22, P=0.301</td>
</tr>
<tr>
<td>Hill’s N1</td>
<td>19</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>4.5 ± 0.57</td>
<td>7</td>
<td>3.8 ± 0.42</td>
<td>12</td>
<td>F(1,8) = 0.45, P=0.521</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Dell Quay</th>
<th>Total n</th>
<th>Pro n</th>
<th>Unpro n</th>
<th>GLM test</th>
<th>Dug n</th>
<th>Undug n</th>
<th>GLM test</th>
<th>Low n</th>
<th>Mid n</th>
<th>GLM test</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>35</td>
<td>11.27 ± 0.94</td>
<td>15</td>
<td>14.90 ± 1.45</td>
<td>20</td>
<td>F(1, 13) = 8.10, P=0.014</td>
<td>14.53 ± 1.42</td>
<td>15</td>
<td>12.45 ± 1.30</td>
<td>20</td>
</tr>
<tr>
<td>n</td>
<td>35</td>
<td>410 ± 100</td>
<td>15</td>
<td>368 ± 60</td>
<td>20</td>
<td>F(1, 12) = 0.13, P=0.730</td>
<td>303 ± 59</td>
<td>15</td>
<td>449 ± 82</td>
<td>20</td>
</tr>
<tr>
<td>Hill’s N1</td>
<td>35</td>
<td>3.6 ± 0.34</td>
<td>15</td>
<td>5.3 ± 0.62</td>
<td>20</td>
<td>F(1, 12) =12.4, P=0.004</td>
<td>5.2 ± 0.65</td>
<td>15</td>
<td>4.1 ± 0.50</td>
<td>20</td>
</tr>
</tbody>
</table>

877

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 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 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 dug/undug; protected/unprotected and low/mid shore; and transect and low/mid shore. Number of individuals (n): protected/unprotected and dug/undug; 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;
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 except Transect 10 were analysed, but only low shore cores were analysed for Fareham Creek.
<table>
<thead>
<tr>
<th></th>
<th>IMD (Dug, undug compared)</th>
<th>Dispersion value (dug)</th>
<th>Dispersion value (undug)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fareham Creek</td>
<td>0.41</td>
<td>0.69</td>
<td>1.10</td>
</tr>
<tr>
<td>Dell Quay</td>
<td>0.33</td>
<td>0.92</td>
<td>1.24</td>
</tr>
</tbody>
</table>

**PERMDISP test**

<table>
<thead>
<tr>
<th></th>
<th>Significance test</th>
<th>Dug</th>
<th>Undug</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fareham Creek</td>
<td>F(1, 17) = 6.72, P (perm) = 0.027</td>
<td>32.7 (3.4)</td>
<td>41.4 (1.6)</td>
</tr>
<tr>
<td>Dell Quay</td>
<td>F(1, 33) = 1.29, P (perm) = 0.335</td>
<td>37.2 (3.2)</td>
<td>43.2 (4.3)</td>
</tr>
<tr>
<td>Sites combined</td>
<td>F(1, 52) = 7.59, P (perm) = 0.019</td>
<td>38.0 (2.0)</td>
<td>45.2 (1.6)</td>
</tr>
</tbody>
</table>

**β diversity**

<table>
<thead>
<tr>
<th></th>
<th>Significance test</th>
<th>Dug</th>
<th>Undug</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fareham Creek</td>
<td>F(1, 17) = 2.42, P (perm) = 0.162</td>
<td>27.9 (2.2)</td>
<td>34.4 (2.4)</td>
</tr>
<tr>
<td>Dell Quay</td>
<td>F(1, 33) = 6.66, P (perm) = 0.026</td>
<td>31.5 (2.8)</td>
<td>39.8 (1.9)</td>
</tr>
<tr>
<td>Sites combined</td>
<td>F(1, 52) = 8.93, P (perm) = 0.01</td>
<td>32.2 (1.9)</td>
<td>39.4 (1.5)</td>
</tr>
</tbody>
</table>

Table 4. Dispersion values for dug and undug communities from each site and calculated Index of Multivariate Dispersion (IMD) scores. Higher dispersion values indicate greater variability and heterogeneity in a community and IMD values are calculated from the comparison between dug and undug areas. Homogeneity of dispersions between dug and undug communities for each site and combined is compared with square root transformation and Bray-Curtis similarity matrix using PERMDISP. β diversity (defined as variability in composition) for dug and undug communities for both sites and combined is calculated using PERMDISP on presence/absence data in conjunction with the Bray Curtis similarity matrix.
### Table 5

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