J. Mar. Biol. Ass. U.K. (2007), **87**, 703–716
Printed in the United Kingdom

doi: 10.1017/S0025315407055026

Effects of bait collection on *Nereis virens* populations and macrofaunal communities in the Solent, UK

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The Solent European Marine Sites contain many tiers of habitat and species conservation, but also high levels of bait collection. Effective management strategies must be founded on up-to-date and locally based information from relevant studies of the impacts; these have been lacking for the collection of *Nereis virens*, a key bait species. The impacts on macrofauna were assessed through two approaches; (a) undug and dug sites in the Solent were compared over two years of repeat sampling; and (b) monitoring the long-term effects of simulated bait collection at an undug site through five years of yearly sampling. Dug sites had significantly higher densities of *N. virens*, but the mean weight was found to be significantly lower than those collected from the undug sites, but percentage maturity was not different. Organic content and sediment particle sizes differed between sites, and only the presence of gravel had a significant positive correlation with density. No clear patterns of other macrofauna species present were evident, although there was a significantly lower density of the terebellid polychaete *Neoamphitrite figulus* at the dug sites. Simulated bait collection did not alter overall macrofauna diversity, but certain species were affected. Abundance of *N. figulus* and the commensal *Harmothoë glabra* remained consistently lower in the dug area, whilst *Cerastoderma edule* numbers were reduced initially, but recovered. Numbers of *Nephtys hombergii* declined in both areas, but at a significantly greater rate in the dug area. A general decline in the abundance of many species, irrespective of digging, occurred over the period. The importance of these changes in *Nereis virens* populations and in the macrofauna community needs to be investigated prior to any management decisions on collection.

INTRODUCTION

Bait collection of polychaetes from soft sediments remains a contentious issue in the UK, but especially in the Solent area of the south coast of England. This area has a high coastal population density and contains a number of internationally important marine sites. Collectively known as the Solent European Marine Sites (SEMS) they include Special Areas of Conservation (SACs); Special Protection Areas (SPAs); Ramsar sites; Sites of Special Scientific Interest (SSSI); and local nature reserves. Intertidal mudflats and sandflats are key habitats for the SACs and a number of sites within the Solent are internationally important for birds (SPAs), and the relevant EU directives require that these are conserved and protected. To ensure that the SEMS remain in a favourable condition, a management scheme has been established and strategies have been suggested for the management of bait collection. However, only the production and distribution of a voluntary bait collection code of conduct has been implemented.

In the UK, lugworms (*Arenicola* spp.) and ragworms (*Nereis* spp.) are the two major polychaete groups collected for bait with *Nereis virens* (Sars) being the most important species (Olive, 1994). It is estimated that at least 1000 tonnes of bait worms are collected per annum, but it is virtually impossible to quantify the trade at national or regional levels because so little is officially recorded (Fowler, 1999). In comparison, the collection of the polychaete *Diopatra neapolitana* (Delle Chiaje) in Canal de Mira, Portugal, was in excess of 45 tonnes per annum (Cunha et al., 2005), whilst the Maine bait fishery peaked at 180 tonnes of *N. virens* and *Glycera dibranchiata* (Ehlers) combined (Creaser et al., 1983). However, both of these surveys were from very localized areas.

Within the Solent region the National Federation of Sea Anglers provided estimates that in 1997 there were as many as 40,000 active sea anglers, but again, accurate numbers are difficult to obtain (Fowler, 1999). Estimates using questionnaires suggest that since the 1970s the number of bait collectors in the Solent has fallen, usually because of declining target fish stocks. There is no firm evidence to suggest that the amount of worms available has changed during this period, but most collectors and anglers agreed that bait abundance had also declined (Fowler, 2001). Coastal development, pollution, sediment erosion/deposition and many other reasons were suggested for the perceived decline.

In the UK the vast majority of bait is collected through manual turning of the sediment with a garden fork. The impacts of this method have received considerable attention, with studies investigating its effects on ecosystems, non-target and target species. Although numbers of small non-target species are often reduced significantly, these usually recover relatively quickly once bait collection has ceased (Harvard & Tindal, 1994). However, significant long-term reductions in population numbers are usually seen in those long-lived, larger and less abundant species (Jackson & James, 1979; Ambrose et al., 1998). There is also evidence that wading bird populations can either be disturbed directly by the presence of bait collectors (Townshend & O'Conner, 1993) or are affected by reductions in key prey species (Shepherd & Boates, 1999).

A number of studies have investigated the impacts on lugworms (e.g. Blake, 1979; McLusky et al., 1983; van den Heiligenberg, 1987; Harvard & Tindal, 1994). Some studies suggest that populations of *Arenicola marina* are robust, and provided digging is not extensive, can repopulate dug areas within approximately one month (Blake, 1979), although there may be differences in the rate of recovery between the mounds and basins produced (McLusky et al., 1983). However, Harvard & Tindal (1994) found that recovery was substantially longer with experimentally dug plots recovering to only 21% of control levels in six months. In contrast, there has been little work on the effects of bait collection on the population structure of *N. virens*. Blake (1978) compared an exploited and unexploited population over one year on the north-east coast of England and found no difference between the monthly size–frequency distributions for 11 months of the year. However, in Blake's study only two sites were sampled and other key physiochemical parameters of the sediment were not investigated. Olive (1993) investigated *N. virens* populations at a number of sites in the Menai Strait, Wales that were all exploited for bait by non-commercial anglers. Sampling in this study was not quantitative, but did find low densities of large individuals present at the sites and up to 20% of these were mature.

Most previous experimental studies on the impacts of bait collection (lugworms and ragworms) have been short term, with manipulated sites and 'naturally occurring' bait collection being monitored for as little as two to three months (e.g. McLusky et al., 1983) or up to one year (e.g. Blake, 1978). Beukema (1995) did undertake a long-term survey (1970–1995) in the Dutch Wadden Sea, but this was in relation to mechanical dredging of lugworms; a method that is not permitted within the UK. As many of the impacted species are relatively long-lived, the short-term studies were not able to assess the recovery from juvenile recruitment, instead focusing mainly on the adult migration phase.

In the Solent an extensive report by Fowler (2001) used subjective discussions and interviews with bait collectors, retailers, regulatory bodies and other interested parties to develop a picture of the extent of bait collection. The benthic surveying component of Fowler's report was also confined to mapping the littoral communities and did not involve direct sampling of the macrofauna or the target species. As a result there are very limited quantitative data of the impacts and extent of bait collection in the Solent. This may lead to management decisions based on information gathered from sources that are not appropriate to the local conditions or habitats.

The juxtaposition of large areas of protected coastal habitat with high levels of bait collection in the Solent gives great scope for conflicts and disputes between relevant parties. In this paper we have approached the issue of bait collection and acquiring baseline data through two methods. Firstly, a two-year macrofaunal survey of a number of sites where regular collection occurs together with undug sites was undertaken to assess any differences in macrofauna diversity and the population structure of *N. virens*. Secondly, using experimentally simulated bait collection in an undug site, we also report on the long-term (five years) changes in comparison to adjacent control (undug) areas.

MATERIALS AND METHODS

Solent bait collection survey

Site selection

After preliminary visits and discussions with local bait collectors, five sites were chosen within the Solent area for sampling (shown in Figure 1). Broadmarsh in Langstone Harbour (50°50.17′N 00°59.38′W), Dell Quay in Chichester

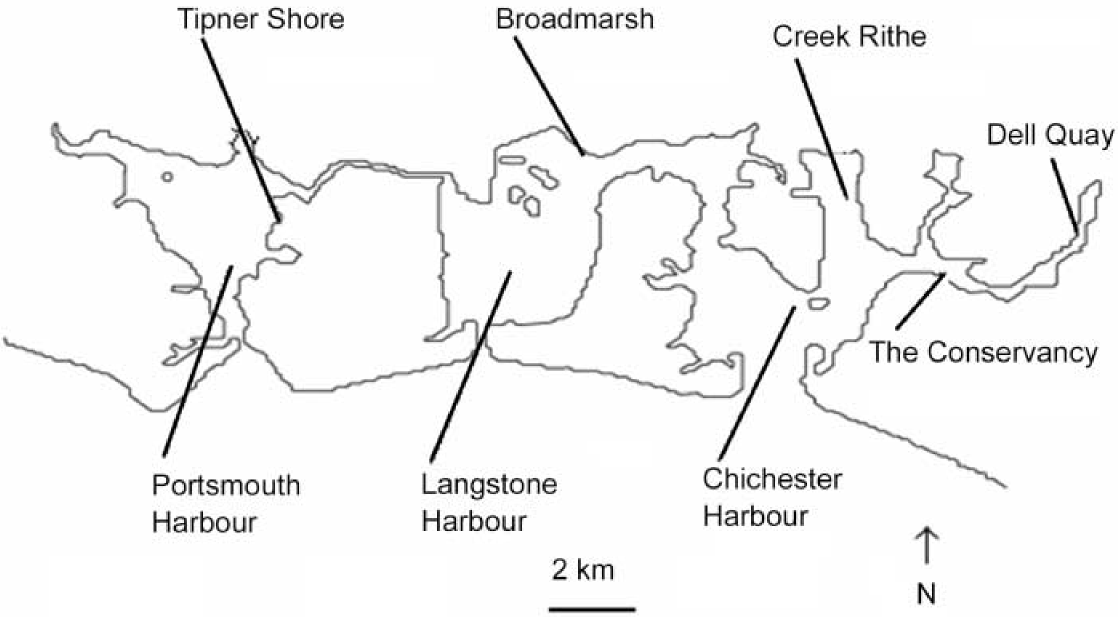


Figure 1. Map of the Solent area including sampling sites (dug: Broadmarsh, Dell Quay and Tipner; undug: The Conservancy and Creek Rithe).

Harbour (50°48.90′N 00°49.01′W) and Tipner Shore in Portsmouth Harbour (50°49.15′N 00°05.31′W) are all dug for bait. Fishbourne Channel (50°48.4′N 00°52.00′W) and Creek Rithe (50°49.10′N 00°53.75′W), both in Chichester Harbour, were free from bait collection activity due to Creek Rithe's inaccessibility and Fishbourne Channel being in front of the Chichester Harbour Conservancy Headquarters (termed 'The Conservancy' from now on) (see Discussion for further elaboration of evidence for being undug sites). All five sites are fully saline and were sampled between November 2004 and March 2005 on low water spring tides. The sampling regime was repeated in December 2005 to March 2006.

Macrofauna sampling and analysis

At each site, as close to the water's edge as possible, five 1 m^2 quadrats were randomly selected and each was dug over using a garden fork to a depth of 30 cm and any visible polychaetes removed (minimum size of 0.3 g). A 20 cm depth of sediment was also removed from a box core (0.0625 m^2) next to each quadrat and then returned to the laboratory for macrofauna sieving. Adjacent to three of the five quadrats, a sediment core (0.0079 m^2, 20 cm deep) was also removed for subsequent particle size and organic content analysis. *Nereis virens* collected from the 1 m^2 quadrat were dried with a paper towel before weighing. Coelomic fluid was also taken from each individual using a 25-gauge hypodermic needle, and examined under a light microscope for the presence of well-developed gametes (late stages of spermatogenesis, i.e. sperm in tetrads or later or oocytes greater than 120 μm). These individuals would be expected to spawn in spring. Any other polychaetes collected from the quadrat were also enumerated and identified. Using running seawater all box cores were then sieved through 2 mm and 0.5 mm sieves. All organisms and sieved sediment retained on the sieves were fixed in 4% formalin in seawater for later sorting and identification.

Particle size and organic content analysis

Only core samples from 2005–2006 were used for particle size analysis due to loss of original material during storage. These samples were heated to 65°C until completely dry. Following the method of Buchann (1984), rapid partial analysis by wet sieving was performed on the sediment from the cylindrical cores. Two hundred and fifty ml of water and 10 ml of sodium hexametaphosphate (6.2 g l^{-1}) were added to 25 g of sediment. This was broken up with a glass rod, stirred mechanically for 15 min, before being soaked overnight and then stirred mechanically for a further 15 min. The sediment suspension was washed onto a 63 μm sieve and 'puddled' until no further material passed through the sieve. The sieve and its contents were then dried at 100°C and were then agitated over white paper until no further material was observed on the paper. The remaining material on the sieve was weighed and this was subtracted from the original weight to give the silt–clay fraction. This material was then put through a sieve-shaker for 15 min before each size fraction was reweighed. The sieve sizes used in micrometres (phi scale in brackets) were: 63 (+4); 90 (+3); 125 (+3); 180 (+2.47); 250 (+2); 500 (+1); 1000 (0); 2000 (−1) and 4000 μm (−2). For organic content, triplicate samples of 20 g of dried sediment were ground with a pestle and mortar, weighed, and then placed in a muffle furnace at 500°C for 4.5 h. Samples were then reweighed to give the mean percentage organic content per sample (Greiser & Faubel, 1992).

Effects of simulated bait digging (Creek Rithe)

Creek Rithe is only accessible by boat on good spring tides and has sloping mud banks on either side with the bed of the channel drying out to firmer homogeneous silt/clay sediment with shingle and large flints. Within the channel bed a 15 m wide and 40 m long area was selected and nominally divided into two areas, either side of the midline of the channel; the eastern side was designated as an 'undug' area, the other as a 'dug' area. A pre-trial survey was then performed (August 1995) across both areas; the large, sessile epifauna were counted using two randomly located 0.25 m^2 quadrats in each half. The density of the larger infauna was determined by digging four 0.5 m^2 areas as above, and the macrofauna species removed (minimum size collected of 0.4 g). Six core samples (three in each area) of 0.00117 m^2 and 15 cm deep were also removed for subsequent sieving through a 1 mm mesh. Two randomly located plots of 2×1 m on the 'dug' area were then marked out with plastic pegs and dug over with a fork and any *N. virens* picked out (minimum size of around 0.3 g) to simulate digging activity. Both the undug and the dug areas were subsequently surveyed in September using the same methods, but with one suite of samples being taken from within each 2×1 m plot from the dug side and four from the undug side. Both areas were then sampled in each successive year until 1999.

Statistical analysis

All data were analysed using Minitab v. 13 and normalized ($\log_{10}$+1, square root or arcsine transformation) and tested for homogeneous variances, where necessary. Differences between years, undug and dug groups of sites, as well as individual sites for the weights, percentage maturity and numbers of *N. virens* and *Neoamphitrite figulus* (Dalyell) were tested using General Linear Modelling (GLM) with site as a nested variable within dug/undug and with subsequent pairwise comparisons, where necessary. Differences in sediment granulometric types between sites and percentage organic content were analysed using a GLM model of a design similar to that used for weights, with subsequent pairwise comparisons. Sediment particle analysis was graphically plotted and the median grain size (Md, μm), phi interquartile range (QDϕ) and phi quartile skewness (Skqϕ) of the data ascertained. Correlations between the amount of a specific size fraction or organic content from the sediment core (three per site) and the number and weight of *Nereis virens* and the numbers of *Neoamphitrite figulus* from the adjacent quadrats (three per site), were also assessed through the calculation of the Pearson product moment correlation coefficient.

Statistical modelling for Creek Rithe was difficult in its original format as the pre-trial August data were common to both the undug and dug sites. Pre-trial data and the undug September 1995 data were, therefore, combined into the 1995 undug data (One-way analysis of variances

(ANOVAs) of the two data sets for all species confirmed that there were no significant differences between them). Differences between dates, sites and interaction for Creek Rithe were then assessed using GLM followed by multiple pairwise Tukey comparisons. Species diversity and equitability of the macrofauna data was measured using the Shannon–Wiener function (H), which was calculated for each sample set and then averaged (Begon et al., 1996).

RESULTS

Solent undug/dug site comparisons

Site descriptions and sediment characteristics

Bait collection at Dell Quay covers an area of approximately 0.25 km^2 and covers both sides of the Fishbourne Channel, but sampling was confined to the eastern side. Bait collection can be heavy, but patchy at this site, and is dug regularly by many collectors resulting in many mounds and troughs. Dell Quay has a small proportion of silt/clay with only 25% finer than 63 μm, 15% of the material is greater than 4000 μm and it has the highest median diameter (Md=1150 μm). Consequently the sediment is very poorly sorted with the highest QDϕ(+2.85) and unlike all the other sites is positively skewed to smaller particle sizes (Skqϕ=+1.05). Cumulative percentage particle size data are presented in Figure 2 for all sites.

Sampling at Tipner was along a corridor (500 m long × 10 m wide) of shore between Portsmouth and Whale Island as it was impossible to access the lower shore due to excessively soft sediment. Sediment at this site has the second highest median diameter of the sites (Md=350 μm) with only 13% of the particles less than 63 μm. The site is more sorted than Dell Quay, but is negatively skewed from the median (QDϕ=+1.9; Skqϕ=−0.5).

The area used for bait collecting at Broadmarsh is approximately 0.5 km^2 and is easily accessed from the shore; consequently the sediment is dug regularly. Particle analysis reveals that the sediment has a high proportion of silt/clay as 45% of the particles passing through the 63 μm sieve. However, the sediment is also poorly sorted with 25% of the material larger than 2 mm and is negatively skewed to the larger particles (Md=63–90 μm; QDϕ=+2.25; Skqϕ=−2.25).

Both the Conservancy Centre and Creek Rithe had no evidence of any previous bait collection. Each sampling area was approximately 100 m long by 20 m wide with large pieces of flint present at Creek Rithe. Although sediment at both these sites also has comparable proportions of silt/clay (55%) and median diameters (Md=63 μm) to Broadmarsh, both are more sorted and less negatively skewed to the smaller particles (Creek Rithe: QDϕ=+0.85; Skqϕ=−0.85; The Conservancy: QDϕ=+0.4; Skqϕ=−0.4).

Sediment particle data were further categorized into four standard granulometric types: silt/clay (<63 μm); sand (63–2000 μm); gravels (2000–4000 μm) and cobbles (>4000 μm), and the data are presented in Figure 3. Analyses of the types using GLM show that there are significant differences between the undug and dug groups of sites and between individual sites. The amount of silt/clay in both Creek Rithe and The Conservancy is high, with nearly half of the sediment being less than 63 μm. This accounts for there being significantly more in the undug sites than the dug sites ($F_{1,14}$=101.94, P=0.000). Site specific differences are also present ($F_{3,14}$=18.07, P=0.000), but the site differences do not separate out into dug and undug groups. Pairwise comparisons show that Broadmarsh, Creek Rithe and The Conservancy are similar and all three have significantly more silt/clay than Dell Quay or Tipner (which are not different from each other). The sand content of the sediment is not significantly different between the undug and dug sites, but there are significant differences between sites ($F_{3,14}$=5.01, P=0.022). Although Tipner has more sand than any of the other sites, it is only significantly different from Broadmarsh, (differences between Tipner and either Dell Quay or Creek Rithe are just not significantly different). Amounts of gravel in the sediments are on the whole low, but highly significant differences still exist between dug and undug sites ($F_{1,14}$=67.33, P=0.000) and also between sites ($F_{3,14}$=13.64, P=0.001). Sediment from The Conservancy and Creek Rithe both have very low levels of gravel and are significantly lower than Dell Quay or

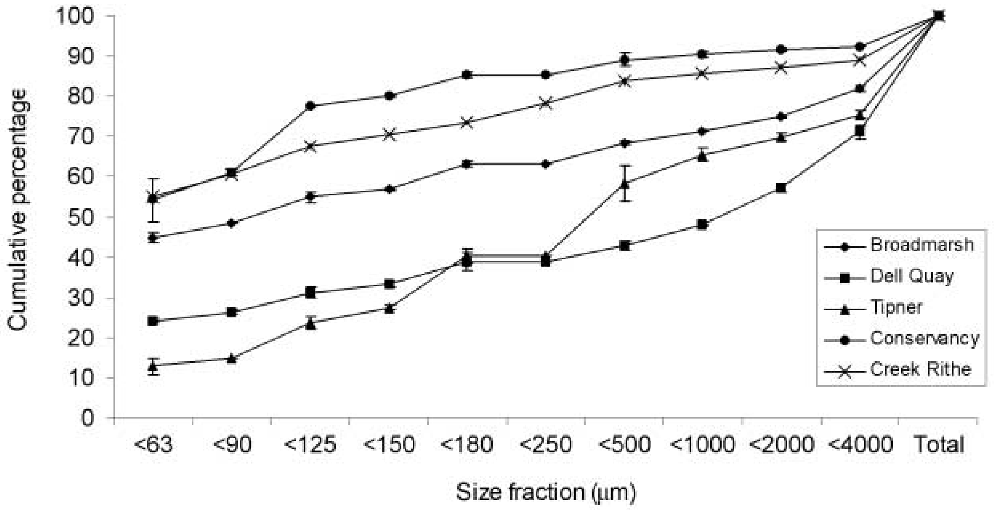


Figure 2. Mean cumulative percentage (±SEM) of the particle size (μm) for the five Solent sites (dug: Broadmarsh, Dell Quay and Tipner; undug: The Conservancy and Creek Rithe). Samples were collected during December 2005–March 2006 using a sediment core (0.0079 m^2, 20 cm deep) and analysed according to the method of Buchann (1984).

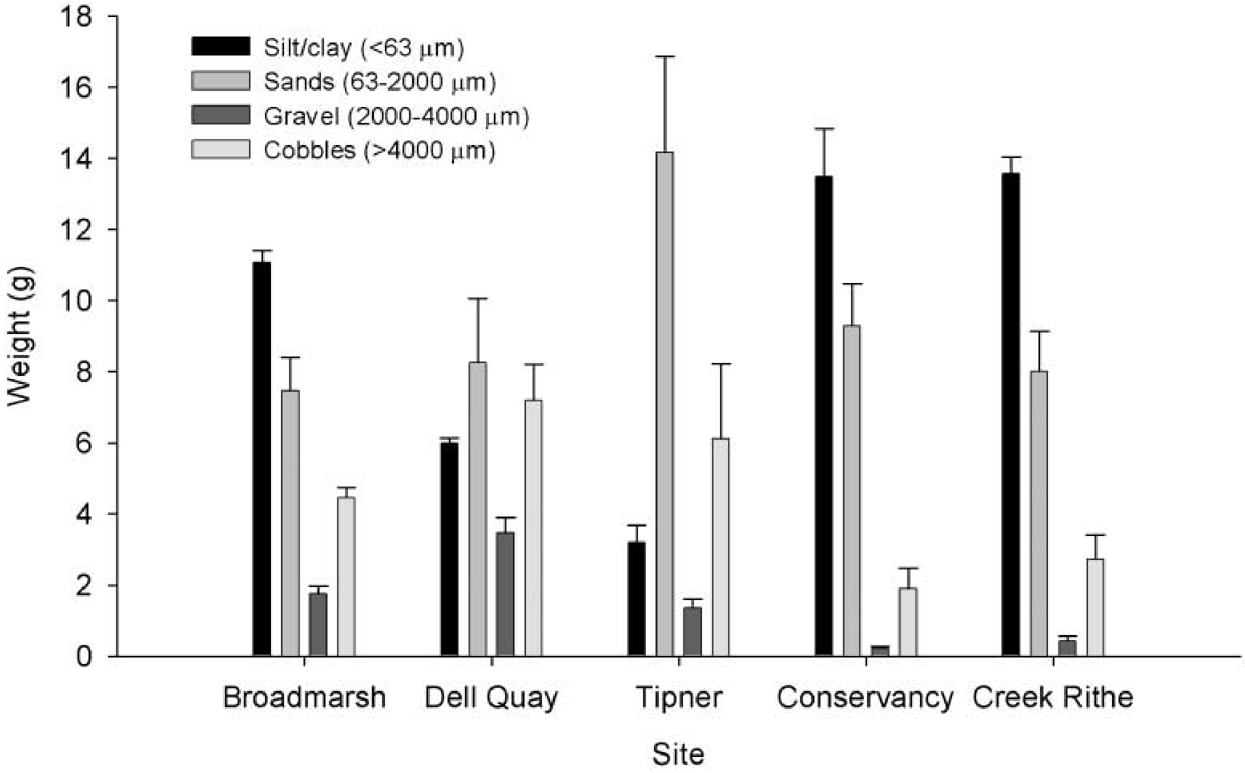


Figure 3. Fractional content of sediment (g) (±SEM) for the five Solent sites (dug: Broadmarsh, Dell Quay and Tipner; undug: The Conservancy and Creek Rithe). Total amount of sediment used during processing was 25 g in all cases.

Broadmarsh, whist Dell Quay has significantly more gravel than either Tipner or Broadmarsh. Again, differences between sites do not always follow the dug/undug groups with no significant differences between Tipner and Broadmarsh, The Conservancy or Creek Rithe in gravel content. Significant differences in the amount of material classified as cobbles are only present between undug and dug sites ($F_{1,14}$=11.88, P=0.006) with significantly more of this material present at the dug sites. However, there are no significant differences between any pairs of sites from either dug or undug locations.

Percentage organic content of the sediment over the two years at the sites ranged from 3.5% at Dell Quay in 2004/2005 to 4.1% at Tipner in 2005/2006. As all measurements fall within this narrow range it is not surprising that statistical analysis confirms there are no significant differences between the undug/dug sites, individual sites, or years.

Macrofauna composition

The mean densities of *Nereis virens* per 1 m^2 quadrat combined over both years are presented in Figure 4 for each site, and for the combined undug and dug sites. A general linear model confirms that there is a highly significant difference between the undug and dug sites ($F_{1,43}$ =27.81, P=0.000) with a mean of 9.87 ±1.59 per m^2 in the dug sites in comparison to 2 ±0.41 per m^2 in the undug sites. There are also significant differences between individual sites ($F_{3,43}$=2.97, P=0.042). Subsequent Tukey's pairwise comparisons show that Creek Rithe has a significantly lower density than any of the dug sites (Tipner, Dell Quay or Broadmarsh), whilst The Conservancy has a significantly lower density than Broadmarsh only. Although there are no significant differences between the two years of sampling, there is interaction between the year and undug/dug sites ($F_{1,43}$=4.67, P=0.036). One modest, but significant positive correlation exists for gravel and the density of *N. virens* (F=0.642, P=0.010).

In contrast to *N. virens,* the combined density of *Neoamphitrite figulus* over the two years is significantly higher at the undug sites (6.35 ±1.84 per m^2) than the dug sites (0.53 ±0.28 per m^2) (GLM $F_{1,43}$=42.41, P=0.000) (see Figure 4). No specimens were found at either Broadmarsh or Tipner for both years and although some specimens were present at Dell Quay in both years, half the quadrats did not contain any individuals suggesting a spatially patchy distribution. Conversely, The Conservancy exhibited temporal changes with no specimens present in 2004/2005, but a mean density of 3.4 ±0.52 per m^2 for 2005/2006. Only Creek Rithe had specimens present in every quadrat for both years, resulting in a significantly higher density (6.35 ±1.84 per m^2) when compared to all the others sites using Tukey's pairwise comparisons. There was also no significant difference between the two years of sampling.

The percentage number of mature *Nereis virens* per quadrat (those with gametes of a size that indicate spawning in the following spring) and the mean worm weight at each site are presented in Figure 5. Although there are no significant differences between the sites or years for the mean worm weight, worms from both The Conservancy and Creek Rithe are, on average, heavier; this results in a significantly higher mean weight at the undug sites (5.76 ±0.71 g) than the dug sites (3.89 ±0.177 g) (GLM: $F_{1,310}$=8.06, P=0.005). There are

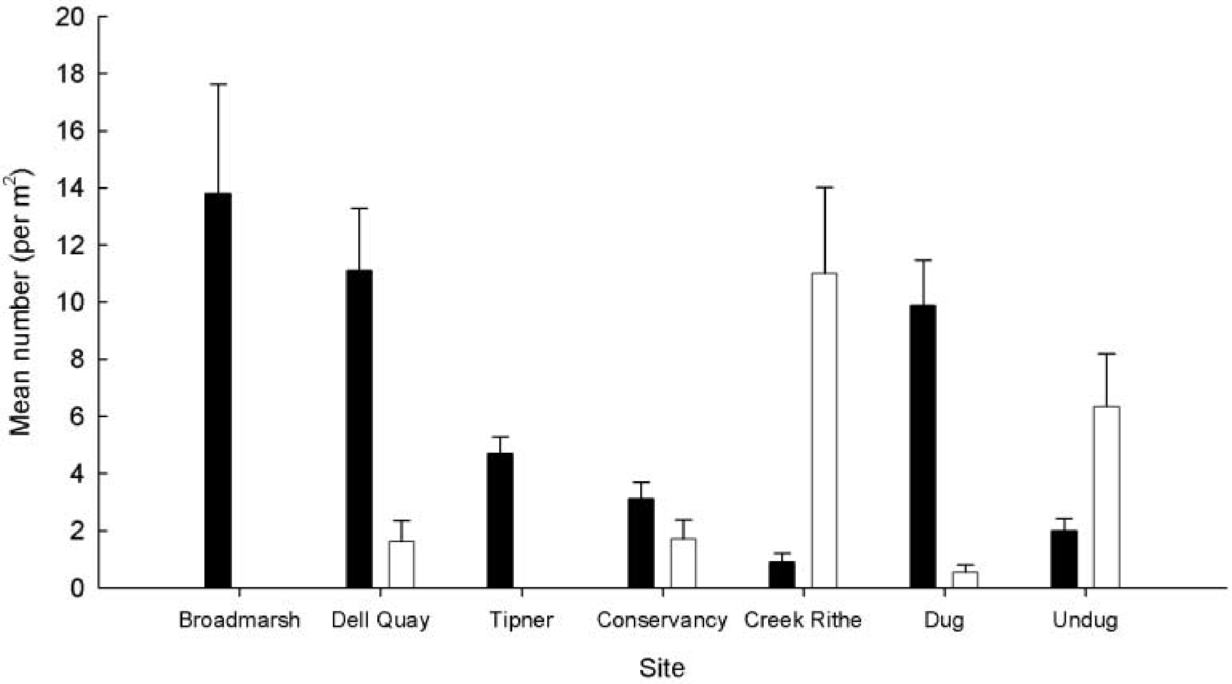


Figure 4. Mean (±SEM) numbers per m^2 of *Nereis virens* (black bars) and *Neoamphitrite figulus* (white bars) from (dug: Broadmarsh, Dell Quay and Tipner and undug: The Conservancy and Creek Rithe) sites; data pooled from two years of sampling. Dug and undug are means of specific sites. Samples were collected between November 2004 and March 2005 and between December 2005 and March 2006 on low water spring tides by digging a 1 m^2 quadrat with a fork and removing all visible animals.

no significant differences between the numbers of mature individuals between the dug and undug sites, individual sites or year. In addition, the mean weight of mature individuals from the dug sites (9.48 ±0.92 g) is not significantly different from those collected from the undug sites (9.19 ±0.97 g).

Macrofaunal species were recorded in the box cores from the five sites over both years and their occurrence at each site (both years combined) is presented in Table 1. At all sites polychaetes are dominant, although significant numbers of crustaceans and molluscs were also present, but Table 1 indicates that Creek Rithe has the most diverse polychaete fauna. No clear patterns can be discerned, although *Anaitides mucosa* (Oersted) was only present at the undug sites and *Harmothoë glabra* (Malmgren) and *H. impar* (Johnston) were only found at

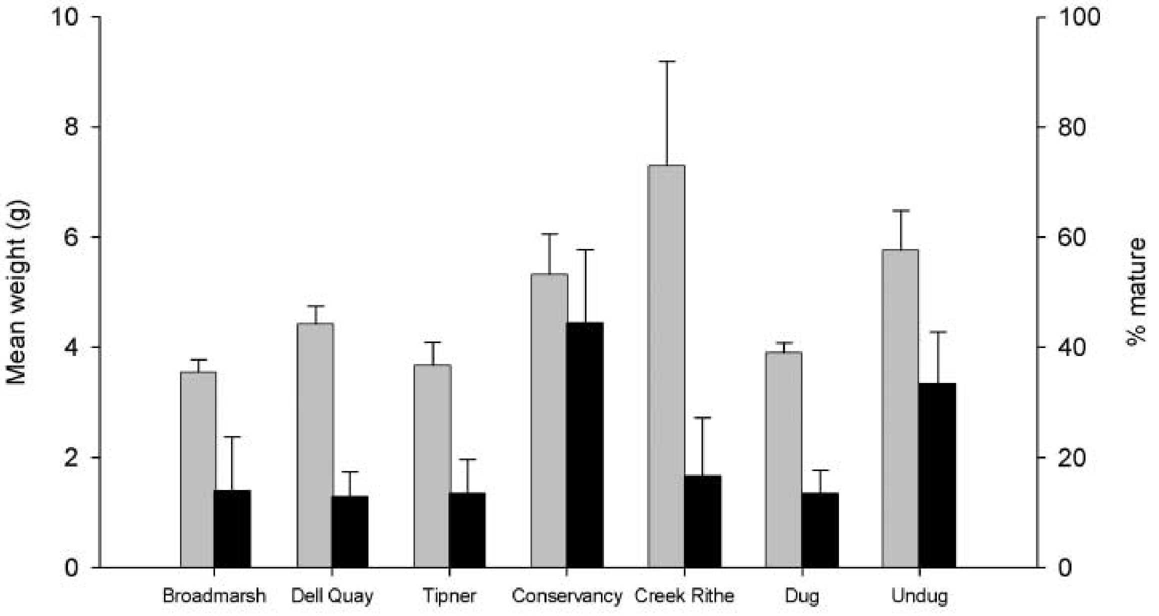


Figure 5. Mean (±SEM) individual weight (g) of the *Nereis virens* collected (grey bars) and the mean percentage (±SEM) number of maturing individuals per quadrat (black bars) from five Solent sites (dug: Broadmarsh, Dell Quay and Tipner and undug: The Conservancy and Creek Rithe); data pooled from two years of sampling. Samples were collected between November 2004 and March 2005 and between December 2005 and March 2006 on low water spring tides by digging a 1 m^2 quadrat with a fork and removing all visible animals.

Table 1. *Presence (+)/absence of macrofauna species collected from box cores (0.0625 m^2) from dug (Broadmarsh, Dell quay and Tipner) and undug (The Conservancy and Creek Rithe) sites pooled from two years of sampling. Samples were collected between November 2004 and March 2005 and December 2005 and March 2006 on low water spring tides. Mean number of species (±SEM) per box core and total number of species per site are also presented.*

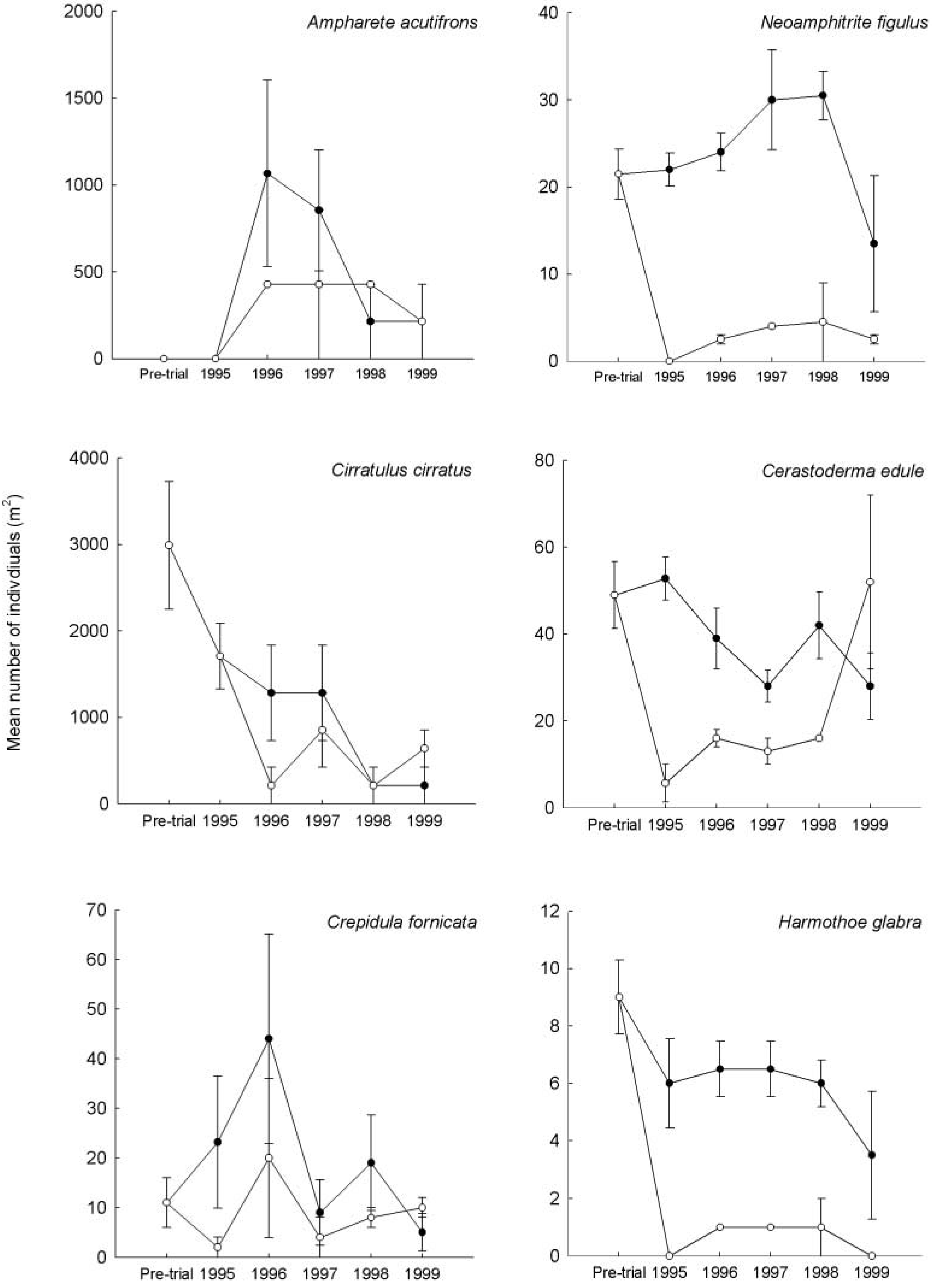
Species	Broadmarsh	Dell Quay	Tipner	Conservancy	Creek Rithe
ANNELIDA					
Anaitides mucosa				+	+
Arenicola marina	+				
Caulleriella zetlandica			+		
Chaetozone gibba	+				+
C. setosa		+			
Cirratulus cirratus	+			+	+
Cirriformia tentaculata	+		+		+
Glycera tridactyla	+	+	+		
Glycera sp.				+	
Harmothoë glabra					+
H. impar					+
Melinna palmata		+	+	+	+
Neoamphitrite figulus		+			+
Nephtys brasiliensis				+	+
N. hombergii	+		+	+	+
N. caeca				+	+
Nereis diversicolor			+		
N. pelagica		+			+
N. virens	+	+	+		
N. zonata	+		+	+	+
Oligochaete		+			
Phyllodocidae indet.					+
Polycirrus sp.		+			
Sthenelais boa					+
Tharynx sp.	+				
CRUSTACEA					
Amphipoda spp.		+			
Anthura gracilis		+			
Carcinus maenas	+	+	+	+	+
Liocarcinus arcuatus		+	+		+
MOLLUSCA					
Cerastoderma edule	+	+	+	+	+
Hydrobia ulvae	+	+	+		+
Littorina littorea					+
Processa sp.		+			
Ruditapes decussatus					+
NEMERTEAN					
Unidentified		+			
Mean no. of species per core	4.5 ±0.65	3.3 ±0.72	4.3 ±1.2	3.2 ±0.63	6.5 ±0.7
Total number of species	11	16	12	10	21

Creek Rithe. In contrast, *N. virens* were only present in the dug sites. There are significant differences between the sites for the mean number of species per core ($F_{3,49}$=6.04, P=0.002), but only Creek Rithe has significantly higher numbers than either Dell Quay or The Conservancy. There are also significantly more species in the second year of sampling ($F_{1,49}$=38.85, P=0.000), but undug and dug sites are not significantly different from each other.

Experimental bait collection (Creek Rithe)

Analysis of the data from the five-year Creek Rithe trial revealed significant effects of simulated bait collection on the numbers of individuals per m^2 of some species. Significant changes over time in both the dug and undug areas are also present and data for the most abundant are presented in Figure 6. Other species present were not in sufficient numbers to perform individual analyses, but did contribute to the total number of organisms (numbers of all species present combined) (also presented in Figure 6). Of the most abundant species, only *Crepidula fornicata* (L.) and *Mytilus edulis* (L.) show no significant change in abundance between sites or dates due to large variations between quadrats and, in the case of *M. edulis* the low numbers collected.

Four species (*Neoamphitrite figulus, H. glabra, Cerastoderma edule* (L.) and *Nephtys hombergii* (Savigny)), show a significant reduction in numbers in the dug area in comparison to the undug area for all years. Both *Neoamphitrite figulus* and *H. glabra* suffer significant reductions when exposed to digging, with numbers for both species dropping to zero in 1995 then


Mean number of indivdiuals (m^2)
Ampharete acutifrons
2000
1500
1000
500
0
Neoamphitrite figulus
40
30
20
10
0
Cirratulus cirratus
4000
3000
2000
1000
0
Cerastoderma edule
80
60
40
20
0
Crepidula fornicata
70
60
50
40
30
20
10
0
Harmothoe glabra
12
10
8
6
4
2
0
Pre-trial
1995
1996
1997
1998
1999

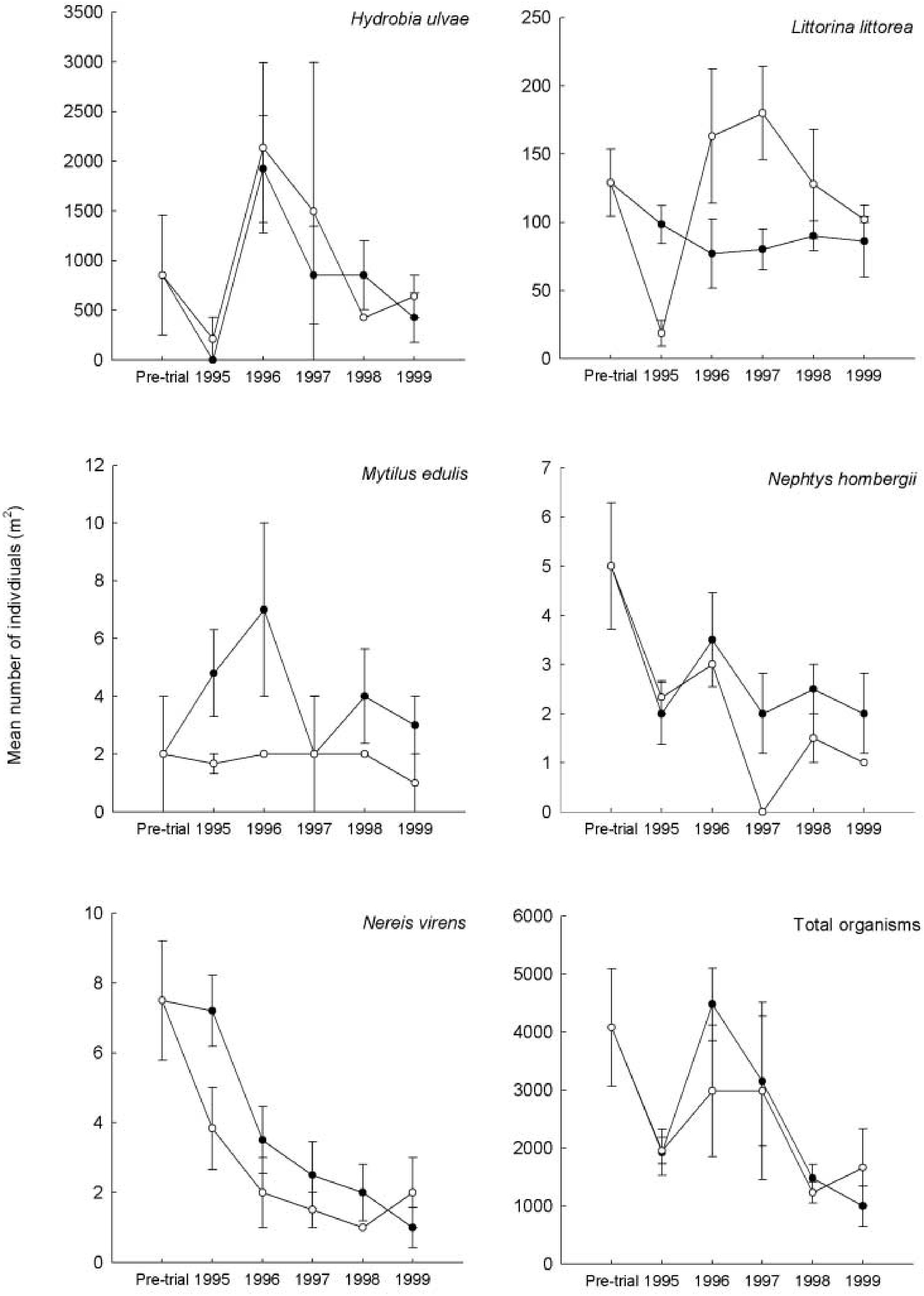


Figure 6. Mean (±SEM) numbers per m^2 (filled circles: undug; open circles: dug area) of the most abundant species and all species combined of macrofauna from the Creek Rithe trial. The pre-trial survey was performed in August 1995 across both dug and undug areas. The large sessile epifauna were counted using four 0.25 mg^2 quadrats, larger infauna by digging four 0.5 m^2 areas with a fork and six core samples of (0.00117 m^2) were also removed for subsequent sieving through a 1 mm mesh. Subsequently, two randomly located plots (2×1 m) on the 'dug' area were dug over and any *Nereis virens* removed to simulate digging activity. Both the undug and the dug areas were subsequently surveyed in September 1995, but with one set of samples (one 0.25 m^2 quadrat, one 0.5 m^2 area and one core sample) being taken from within each 2×1 m plot for the dug side and four sets of samples from the undug area. Both areas were then sampled in each successive year until 1999.

recovering slightly in subsequent years (GLM; $F_{1,24}$=133.9, P=0.000; $F_{1,24}$=57.04, P=0.000, respectively). In both the dug and undug areas, there are no significant effects of date. Over the whole trial period digging also reduces numbers of *Nephtys hombergii* significantly (GLM; $F_{1,24}$=4.57, P=0.042), but numbers in dug and undug areas only began to diverge after 1996. Numbers of *C. edule* dropped dramatically after digging began, but recover in subsequent years (GLM; $F_{1,24}$=29.88, P=0.000), whilst numbers in the undug areas steadily decline (GLM; $F_{4,24}$=3.06, P=0.035).

For all other species, there are no significant differences in the numbers per m^2 between the dug and undug areas, but there are significant changes over the years. Numbers of *Nereis virens* steadily declined in both areas over the period (GLM; $F_{4,24}$=4.76, P=0.005) and *Cirratulus cirratus* (Müller) also showed similar changes (GLM; $F_{4,24}$=3.2, P=0.023). Other species showed a more variable response over the five-year period, often with significant variability between sampling replicates. In both areas, numbers of *Hydrobia ulvae* (L.) fell in 1995, but increased rapidly in the following year before declining back to near pre-trial levels (GLM; $F_{4,24}$=3.51, P=0.016). *Littorina littorea* in the dug area also followed a similar pattern with a reduction followed by a rapid rise in 1996 and then a general decline (GLM; $F_{4,24}$=2.77, P=0.049). In 1995 no *Ampharete acutifrons* (Grube) were collected, but subsequently, numbers rapidly increased in both areas before declining again. Although the mean number of organisms is not significantly different between the dug and undug areas, assessment of diversity using the Shannon–Wiener value (H), confirms that the dug area has a significantly lower mean value (H=0.5536 ±0.074) than the undug area (H=0.8105 ±0.069), (GLM; $F_{1,34}$=9.48, P=0.005).

Irrespective of whether an area was dug or undug, it is clear that Creek Rithe experienced a general decline in the abundance of macrofauna species over the five-year period. Of the 11 species presented in Figure 6, only three (*Cerastoderma edule*, *A. acutifrons* and *M. edulis*) have higher abundances in 1999 when compared to the pre-trial levels and analysis of the mean total number of organisms confirms that this decline was significant (GLM; $F_{4,24}$=2.98, P=0.038). Both areas decreased in 1995, recovered to pre-trial levels for the undug area only, before steadily declining to levels of approximately 25% of the pre-trial numbers. However, in contrast to the decline in the abundance of organisms over the five-year period, there is a significant increase in the Shannon–Wiener index from the pre-trial value to 1999 (GLM; $F_{4,25}$=9.48, P=0.005), but this is only due to the pre-trial value being significantly lower than the 1999 value.

DISCUSSION

Comparison between dug and undug sites

Due to the time constraints of the project it was not feasible to collect information on the levels of digging at the sites, but Broadmarsh, Dell Quay and Tipner have all been consistently dug for many generations by bait collectors (Fowler, 1999). There is evidence of recent extensive and regular digging of up to five individuals per site at any given time at Dell Quay and Tipner and up to ten at Broadmarsh (G.J. Watson, personal observation). In comparison, Blake (1978) reported peak numbers of around 120 diggers in an area of 8000 m^2. However, this was during the summer months and numbers observed during the winter period were similar to this study.

Chichester Harbour Conservancy office is located directly in front of The Conservancy sampling site. There have been no reports of any activity for ten years at this site and officers have also reported no digging at Creek Rithe during their many visits over the years (de Poitier, personal communication). During this study no bait diggers were seen during the numerous visits to both sites or during the five-year simulated study at Creek Rithe. In addition, there was no physical evidence of digging, which would leave sediment changes that are visible for many months in these low energy environments (McLusky et al., 1983). To the best of our knowledge, both sampling sites have not been dug for many years and prior to this any digging have been localized one-off events by one or two individuals. These two sites can, therefore, be assumed to be undug areas in the Solent area.

Data obtained during this study reveal that those sites subjected to digging support a significantly higher density of *Nereis virens* than those that have not been dug, with Broadmarsh, the area that anecdotal observations suggest has the highest digging intensity, supporting the greatest numbers. The dug sites may be supporting higher densities, but the mean weights of those worms collected are significantly smaller than those from the undug sites. A study by Miron & Desrosiers (1990) in the St Lawrence estuary confirmed that the density of *N. virens* increases with intertidal level in an onshore direction and that body-weight distribution followed an opposite pattern. Other studies by Snow & Marsden (1974) and Ambrose (1986) have also observed this relationship. The tidal range in the harbours where the samples were collected is only 4.5 m on extreme spring tides and all have a mean low water springs (MLWS) of 1 m. All sites were sampled within 0.5 m of MLWS and there were no significant correlations between tidal height and the number or mean weight of *N. virens*. In this study the tidal height of sampling was not, therefore, a determining factor of the population of *N. virens* at these Solent sites. The relationships may also be site specific as Bass (1970) found an opposite relationship to that found by Miron & Desrosiers (1990) or it may be linked to other factors such as sediment type and organic content.

Sediment type is usually considered important for the distribution of marine macrobenthos (Nichols, 1970; Thomas, 1987). However, evidence of the roles of the different size fractions and organic content in determining the densities of polychaetes is not consistent. Kennedy (1984) stated that the proportion of sand, silt or clay does not influence polychaete densities whereas Wieser (1959), Bass (1970) and Miron & Desrosiers (1990) gave them an important role. Experimentally, *N. virens* has a clear preference for organically poor (0.7%) sand, but this was not observed in the distributions recorded in the field (Kristensen, 1988), but other field surveys have found a preference (Rasmussen, 1973). In this study, all of the five sites were anoxic and the organic content of each site was relatively high, but not significantly different from each other: ranging between 3.5% and 4.1% over all sites and both years. There was also no correlation between the organic content of the quadrats and the density and size of the *N. virens*.

Although hydrogen sulphide (HS^-) levels were not measured in this study, Miron & Kristensen (1993) found that the density of *N. virens* increased as the HS^- concentration was reduced in the sediment pore water of Danish fjords. Increasing organic enrichment is strongly correlated with the extent of anoxia and increasing sulphide concentrations (Llanso, 1991). As all the sites had very similar levels of organic material and all were clearly very anoxic HS^- concentrations may have been high, but it is unlikely that they differed significantly between them. Miron & Kristensen (1993) also found that a station with the highest HS^- concentration (1715 μM, organic content 15.8%) had the second highest density of *N. virens* (nearly 100 per m^2), very similar to stations with a concentration of only 6–7 μM. These authors acknowledge that whilst sulphide is important, it is strongly correlated with other factors (e.g. grain size and species competition) and is difficult to dissociate from these in the field.

From this study organic content (and associated sulphide concentrations) is not a specific determining factor for differences in *N. virens* populations at these sites. This may be due to other factors specific to a particular site and may also explain the conflicting results from other studies highlighted above. Kristensen (1988) suggested that the high numbers found in organically rich areas was due to individuals dispersing from the surrounding sandflats. Alternatively, high organic content is often associated with a higher fractional content of smaller particles and so it may be difficult to separate out organic content from the sediment particle size distribution. Miron & Desrosier (1990) and Bass (1970) both show that larger individuals require the sediment to be more compact (smaller particle sizes) and, therefore, easier to construct burrows using specific methods for muddy cohesive sediments such as mechanically efficient crack propagation (Dorgan et al., 2005). In this study the undug sites have significantly higher silt/clay content than dug sites, but this does not influence the number of *N. virens*. Differences between the sites and dug/undug groups of sites and the amounts of other size fractions are also present, but the only significant positive correlation is gravel and *N. virens* density. Large particles reduce compaction and create spaces; this may explain why the presence of gravel even within muddy sediment supports higher numbers of smaller individuals that use interstitial spacing for movement (Miron & Desrosiers, 1990). However, a site located within Poole Harbour (the western end of the Solent) and sampled by the authors using the same methodology, had a much higher mean density of 19.6 ±6.7 *N. virens* per m^2. This site had a similar organic content (3.5%), but was exceptionally muddy with 91% silt/clay and less than 1% gravel confirming that the sediment/population relationship is complex.

Nereis virens were significantly smaller than those from the undug sites; the mean individual weights from Broadmarsh, Dell Quay and Tipner were 3.5, 4.4 and 3.7 g respectively compared to 5.3 g for The Conservancy and 7.3 g at Creek Rithe. In comparison, 76% of worms sampled in the St Lawrence estuary weighed less than 200 mg (Miron & Desrosiers, 1990). Densities of these small sized worms were found to be up to 496 per m^2 (Miron & Desrosiers, 1990), 850 per m^2 in Maine, USA (Ambrose, 1986) and over 1000 per m^2 in some stations from a Danish fjord (Kristensen, 1988). The quadrat sampling method used here may miss these small sizes, as it requires the visual location of individuals after turning over the sediment. Nevertheless, worms as small as 0.3 g were collected and the numbers collected, of any size, from the associated box cores (which should sample high densities of small sizes) were found to be only a maximum of 20 per m^2 when converted (data not shown). This confirms that the sampling strategy has not missed smaller sized worms; they are just not present. A number of factors are probably responsible for the large discrepancies in density and size distribution between these studies and the results presented here. The time of sampling has important impacts on accessibility (the worms are much deeper in the winter). This study did also not sample higher up the shore, which was the juvenile/nursery areas in the sampling areas studied by Miron & Desrosiers, (1990). However, a study within the UK by Blake (1978) found between 1 and 3 per m^2 in November and January at sites near Newcastle upon Tyne, which seems to be a more comparable figure.

Although Blake (1978) found that the monthly size–frequency distribution between an exploited and an unexploited population was not significantly different, it is clear from data presented in this study that those Solent sites experiencing bait collection support a higher density of smaller *N. virens* individuals. Nereid polychaetes, including *N. virens*, are well known for their aggressive behaviour (Reish & Aloshi, 1968). This is often associated with defence of burrows and feeding areas (Evans, 1973; Miron et al., 1992a,b). Intra-specific competition and cannibalism have been described as highly important mechanisms regulating adult populations and are considered a major source of mortality (Kristensen, 1984; Miron et al., 1992a) and this competition is even present at the nectochaete stage (Lewis et al., 2003). Digging efficiency through mark and recapture methods was estimated by Blake (1978) and found to be very high (75–80% success) for large worms (>18 cm) but only 2–10% for worms less than 6 cm. Combining this with the desirability of larger worms, bait collection will always inherently select for the larger individuals. Consistent removal of this size-group is likely to enhance the survivorship of smaller individuals through the reduction of intraspecific competition and so support a higher population. A sub-tidal component to the populations (present at other UK sites [Last, personal communication]) that can constantly recruit to the dug area may also maintain relatively high numbers.

Populations of *N. virens* in the UK usually spawn in spring (Brafield & Chapman, 1967; Williams & Bentley, 2002; Watson et al., 2003) with personal observations by the authors showing that between late February and early March is typical in the Solent. Although some of the sampling dates were at the beginning of March, no spent females were collected (these are known to survive for up to a month after spawning [G.J. Watson, personal observation]) and gravid individuals were still present at all sites. We are, therefore, confident that sampling occurred prior to any major spawning activity and the numbers of mature individuals are representative of the population prior to spawning.

Between 12 and 44% of the individuals from each quadrat had mature gametes, with the dug sites having fewer (but not significantly) mature individuals than the undug sites when combined. The 33% of individuals that were mature from the quadrats at undug sites is higher than the 20% frequency observed by Olive (1993) for a population in Wales and the 15% overall percentage of gravid individuals in the intertidal zone from the St Lawrence estuary (Miron & Desrosiers, 1990). Brafield & Chapman (1967) estimated that the majority of worms over two years old would spawn (weighing approximately 7 g). Peak collection for *N. virens* occurs in the summer prior to the spawning and sizes much smaller than this are easily harvested. Collectors are, therefore, likely to remove the majority of those that would normally spawn in the following spring, accounting for the lower numbers of mature individuals present at the dug sites. Evidence from many species that are exploited suggests that individuals are selected for that breed at a smaller size/age (Jennings et al., 2001). Although the mean weights of mature individuals at the dug and undug sites are not significantly different, the relatively low numbers collected here necessitates a much more detailed study to confirm any selective pressure.

Neoamphitrite figulus was the other large polychaete collected from the 1 m^2 quadrats, and data demonstrate a significantly higher density at undug sites than dug sites. In two out of the three dug sites this terebellid was absent and at Dell Quay it was present in only half of the quadrats. Significant numbers were present at Creek Rithe in every quadrat in both years and although significant numbers were recorded at The Conservancy in 2005/2006, no individuals were present in the first year of sampling. These site results suggest a very patchy temporal and spatial distribution. Personal observations at Dell Quay suggest that some areas of sediment had no evidence of previous digging and this may account for the spatial distribution seen at this site. At The Conservancy, sampling in 2005/2006 compared to 2004/2005 was on a lower spring tide, therefore, allowing access to a population that was submerged in the previous year. Feeding and tube building of this species are typical for large terebellids (Blegvad, 1915), but its reproductive habits are unknown (Thorson, 1946). Personal observations by the authors confirm that *N. figulus* require undisturbed and stable sediment and are also fragile and so any damage usually results in death. These are likely to be the key reasons for its disappearance from sites that are regularly used for bait collection.

All the macrofauna collected from the box cores were identified and enumerated, but there is no easily discernible pattern between dug and undug sites for species presence. From the results it became evident that the numbers of individuals of most species collected per box core were low and variable. Other studies have used smaller cores for sampling macrofauna (e.g. Flach, 1992; Brown & Wilson, 1997), but only a list of macrofauna species is presented here as the numerical data collected would not be sufficient to perform valid comparisons of abundance. A more extensive box core survey is required as these differences may be an artefact of the sampling regime and sediments are well known for their heterogeneity of their macrofauna (Kaiser et al., 2001).

Experimental bait collection (Creek Rithe)

Results presented here are the first to show that some large, long-lived species do not recover for a number of years in response to manual bait collection. *Neoamphitrite figulus* and the polynoid scaleworm *Harmothoë glabra* both suffered immediate declines to near-zero levels once digging had occurred, and remained at this level for the whole sampling period. Many polynoid species live commensally with terebellids (Davenport, 1953), and this is the likely relationship between these two species as *H. glabra* was only found within burrows of *N. figulus*. It is not clear if all individuals' burrows are inhabited, but it is likely that *H. glabra* would also die if its host were lost. The failure of these species to recolonize the dug area is due to the near-sessile nature of *N. figulus* that will preclude migration from undug areas. The failure of numbers to recover over the five-year period also suggests that once dug, the area becomes unsuitable for larval settlement, however, the reproductive mode and larval requirements are not known (Thorson, 1946).

The rapid decline in *Cerastoderma edule* after digging was not unexpected, as previous studies have shown that they suffer significant mortality (Jackson & James, 1979; Beukema, 1995; Ambrose et al., 1998). However, the rapid increase in 1999 is surprising, but may be due to the heterogeneous nature of the sediment, highlighted by the large standard errors.

The decrease seen for *Littorina littorea* in 1995 is likely to be due to burial of the adults in the spoil, but the increases in the following years may be due to migration into these dug areas. Personal observations by the authors have shown that epifauna are common on parts of the shore within the Solent harbours that have many stones and other objects on the surface. Digging at Creek Rithe exposed large irregular flints and these could provide significantly more refuges for this species. The gradual decline may be because the flints were subsequently re-covered by sediment.

Other macrofauna, including *Nereis virens,* were not affected by the digging suggesting that these species can re-colonize the area rapidly by adult migration or larval recruitment as has been shown for *Arenicola marina* (Blake, 1979; Olive, 1993; Harvard & Tindal, 1994). The exception was *Nephtys hombergii*, a very mobile species, but which still experienced a decline in the dug sites towards the end of the study period (1997 onwards) and the reasons for this remain unclear.

The losses of species from the dug area contributed to the significant decrease in diversity in comparison to the undug area, even though the total number of organisms does not differ. Studies on lugworms have also reported a loss of diversity, but these have been inferred from the loss of species and biomass and not through the calculation of a diversity index (Beukema, 1995; Brown & Wilson, 1997). Superimposed on this reduction is a decline over the five years in the abundance of most species in both areas. The reasons for this are not obvious, but it may be a local environmental or other external factor that has changed.

Management recommendations

Bait collection and conservation in the Solent continues to be a major issue for the regulatory bodies. The pressure on remaining sites is likely to increase through further restrictions and as other factors contribute to the perceived decline in bait and bait-collecting areas. The evidence presented in this paper provides baseline information to build a management strategy for bait collection in the SEMS and other sensitive areas in the UK, but also raises a number of key questions that must be addressed prior to implementation. It should be noted that these results relate to the impacts on the macrofaunal community only, and that many other important factors need to be taken into account in the decision making process.

Populations of *N. virens* are not reduced by bait collection, and paradoxically, this activity may enhance numbers, although the size distribution of the population is altered. Sediment characteristics may account for some of the differences between sites, but the reduction in intraspecifc competition by bait collectors preferentially removing the larger worms and the sub-tidal population providing sufficient larval and adult supply means that present levels of collection are likely to be sustainable at these sites. Not only is *N. virens* collected for bait but it also plays an important role in intertidal communities (Commito & Shrader, 1985) and is a prey species of many birds (Ambrose, 1986), fish and crustaceans (McIntosh, 1908–1910). The impact of population changes may have wider long-term repercussions that need to be investigated.

The effects of bait collection on macrofauna diversity and total abundance are not unequivocal. What is unambiguous is that specific species (*Neoamphitrite figulus, H. glabra*) decline or disappear in areas where digging occurs. Evidence presented here supports previous work on bait collection (Jackson & James, 1979; Ambrose et al., 1998) and on similar activities such as cockle raking (Kaiser et al., 2001) and mechanical cockle harvesting (Ferns et al., 2000) that those long-lived, larger and less abundant species suffer significant long-term reductions. Mudflats within SACs must be maintained in a favourable condition relative to a baseline, and the macrofaunal communities are key sub-features (European Union Council Directive 92/43EEC). If the losses are detrimental to the functioning of the ecosystem or the species are significant prey items then bait collection on the grounds of the impacts on these macrofauna would not be acceptable. There is no evidence that either species are prey items for birds or fish, although experimental studies have shown some terebellid bodies are palatable to fish (Kicklighter et al., 2003). It is, therefore, vital that the role of these species in an ecosystem be elucidated, prior to any management decisions.

A number of management initiatives have been suggested to reduce conflicts or mitigate the effects of bait collection on macrofauna. Spatial or temporal zonation is often cited as a method to preserve bait stocks, reduce the impacts on macrofauna and sediments, as well as a method of allowing damaged habitats (and presumably the species within) to recover. In particular, a rotating system where different parts of the site are closed, has gained support with the idea that these areas may act as sources of recruitment for the exploited species (Fowler, 1999). The results from the three dug sites indicate that *Nereis virens* can be maintained at levels acceptable for collection without management (although the wider impacts of the population changes are not known). Nevertheless, some other macrofauna species are impacted immediately and may take many years to recover even if bait collection is suspended. Permanent no-take zones may be the best option for preserving these species, but it is unlikely that areas still subjected to bait collection will regain those species lost, as it is the continued disturbance that precludes the species. Ultimately, the ecological benefit of any management scheme must be tested scientifically *before* implementation. It must then also take into account a wide range of social, economic and other ecological issues to effectively manage the resource now, and in the future.

The authors thank and acknowledge the financial support of the SEMS Management Group and the Chichester Harbour Conservancy for the project. The authors thank R. Wilde, M. Sims and M. Godfrey for help with the collection and processing of the samples and Chichester Conservancy for permission to collect samples and the loan of their boat. The authors also thank Karen Hamilton for help with the identification.

REFERENCES

Ambrose, W.G., 1986. Estimate of removal rate of *Nereis virens* (Polychaetea: Nereidae) from an intertidal mudflat by gulls (*Larus* spp.). *Marine Biology*, **90**, 243–247.

Ambrose, W.G., Dawson, M., Gailey, C., Ledkovsky, P., O'Leary, S., Tassinari, B., Vogel, H. & Wilson, C., 1998. Effects of baitworm digging on the soft-shelled clam *Mya arenaria* in Maine: shell damage and exposure on the sediment surface. *Journal of Shellfish Research*, **17**, 1043–1049.

Bass, N.B., 1970. *Aspects of the ecology, behaviour and life history of the polychaete* Nereis virens *Sars*. PhD thesis, University of London, London, UK.

Begon, M., Harper, J.L. & Townsend, C.R., 1996. *Ecology: individuals, populations and communities*, 3rd edn. Oxford: Blackwell Science.

Beukema, J.J., 1995. Long-term effects of mechanical harvesting of lugworms *Arenicola marina* on the zoobenthic community of a tidal flat in the Wadden Sea. *Netherlands Journal of Sea Research*, **33**, 219–227.

Blake R.W., 1978. On the exploitation of a natural population of *Nereis virens* Sars from the North-East Coast of England. *Estuarine and Coastal Marine Science*, **8**, 141–148.

Blake, R.W., 1979. Exploitation of a natural population of *Arenicola marina* (L.) from the North-East coast of England. *Journal of Applied Ecology*, **16**, 663–670.

Blegvad, H., 1915. Food and conditions of nourishment among communities of invertebrate animals found on or in the sea bottom in Danish Waters. *Reports of the Danish Biological Station*, **22**, 41–78.

Brafield, A.E. & Chapman, G., 1967. Gametogenesis and breeding in a natural population of *Nereis virens*. *Journal of the Marine Biological Association of the United Kingdom*, **47**, 619–627.

Brown, B. & Wilson, W.H., 1997. The role of commercial digging of mudflats as an agent for change of infaunal intertidal population. *Journal of Experimental Marine Biology and Ecology*, **218**, 49–61.

Buchann, J.B., 1984. Sediment analysis. In *Methods for the study of marine benthos* (ed. N.A. Holme and A.D. McIntyre), pp. 41–65. Oxford: Blackwell Scientific.

Commito, J.A. & Shrader, P.B., 1985. Benthic community response to experimental additions of the polychaete *Nereis virens*. *Marine Biology*, **86**, 101–107.

Creaser, E.P., Clifford, D.A., Hogan, M.J. Jr & Sampson, D.B., 1983. A commercial sampling program for sandworms *Nereis virens* Sars, and bloodworms, *Glycera dibranchiata* Ehlers, harvested along the Maine Coast. *NOAA Technical Report NMFS SSRF-767*, 56 pp.

Cunha, T., Hall, A. & Queiroga, H., 2005. Estimation of the *Diopatra neapolitana* annual harvest resulting from digging activity in Canal de Mira, Ria de Aveiro. *Fisheries Research*, **76**, 56–66.

Davenport, D., 1953. Studies in the physiology of commensalisms. IV. The polynoid genera *Polynoë*, *Lepidasthenia* and *Harmothoë*. *Journal of the Marine Biological Association of the United Kingdom*, **32**, 273–288.

Dorgan, K.M., Jumars, P.A., Johnson, B., Boudreau, B.P. & Landis, E., 2005. Burrow extension by crack propagation. *Nature, London*, **433**, 475.

European Union Council Directive 92/43EEC, 1992. On the conservation of natural habitats and wild fauna and flora.

Evans, S.M., 1973. A study of fighting reactions in some Nereid polychaetes. *Animal Behaviour*, **21**, 138–146.

Ferns, P.N., Rostron, D.M. & Siman, H.Y., 2000. Effects of mechanical cockle harvesting on intertidal communities. *Journal of Applied Ecology*, **37**, 464–474.

Flach, E.C., 1992. Disturbance of benthic infauna by sediment-reworking activities of the lugworm *Arenicola marina*. *Netherlands Journal of Sea Research*, **30**, 81–89.

Fowler, S.L., 1999. Guidelines for managing the collection of bait and other shoreline animals within UK marine special areas of conservation. *Report to English Nature UK Marine SACs Project*, 112 pp.

Fowler, S.L., 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 and Poole Bay Natural Area. *Report to English Nature and the Bait Collection Steering Group*, 52 pp.

Greiser, N. & Faubel, A., 1992. Biotic factors. In *Introduction to the study of meiofauna* (ed. R.P. Higgins and H. Thiel), pp. 79–114. Washington DC: Smithsonian Institution Press.

Harvard, M.S.C. & Tindal, E.C., 1994. The impacts of bait digging on the polychaete fauna of the Swale Estuary, Kent, UK. *Polychaete Research*, **16**, 32–36.

Heiligenberg T. van den, 1987. Effects of mechanical and manual harvesting of lugworms *Arenicola marina* (L.) on the benthic fauna of tidal flats in the Dutch Wadden Sea. *Biological Conservation*, **39**, 165–177.

Jackson, M.J. & James, R., 1979. The influence of bait digging on cockle, *Cerastoderma edule*, populations in north Norfolk. *Journal of Applied Ecology*, **16**, 671–679.

Jennings, S., Kaiser, M.J. & Reynolds J.D., 2001. *Marine fisheries ecology.* Oxford: Blackwell Science.

Kaiser, M.J., Broad, G. & Hall, S.J., 2001. Disturbance of intertidal soft-sediment benthic communities by cockle hand raking. *Journal of Sea Research*, **45**, 119–130.

Kennedy, V., 1984. A summer benthic survey in Conception Bay, Newfoundland, emphasizing zoogeography of annelids and amphipods. *Canadian Journal of Zoology*, **63**, 1863–1869.

Kicklighter, C.E., Kubanek, J., Barsby, T. & Hay, M.E., 2003. Palatability and defense of some tropical infaunal worms: alkylpyrrole sulfamates as deterrents to fish feeding. *Marine Ecology Progress Series*, **263**, 299–306.

Kristensen, E., 1984. Life cycle, growth and production in estuarine populations of the polychaete *Nereis virens* and *N. diversicolor*. *Holarctic Ecology*, **7**, 249–256.

Kristensen, E., 1988. Factors influencing the distribution of Nereid polychaetes in Danish coastal waters. *Ophelia*, **29**, 127–140.

Lewis, C., Olive, P.J.W. & Bentley, M.G., 2003. Pre-emptive competition as a selective pressure for early reproduction in the polychaete *Nereis virens* Sars. *Marine Ecology Progress Series*, **254**, 199–211.

Llanso, R.J., 1991. Tolerance of low dissolved oxygen and hydrogen sulphide by the polychaete *Streblospio benedicti* (Webster). *Journal of Experimental Marine Biology and Ecology*, **153**, 165–178.

McIntosh, W.C., 1908–1910. *British marine annelids*, vol. 2. London: The Ray Society.

McLusky, D.S., Anderson, F.E. & Wolfe-Murphy, S., 1983. Distribution and population recovery of *Arenicola marina* and other benthic fauna after bait digging. *Marine Ecology Progress Series*, **11**, 173–179.

Miron, G.Y. & Desrosier, G.L., 1990. Distributions and population structures of two intertidal estuarine polychaetes in the lower St Lawrence Estuary, with special reference to environmental factors. *Marine Biology*, **105**, 297–306.

Miron, G., Desrosiers, G. & Retière, C., 1992a. Organisation of fighting in the polychaete *Nereis virens* (Sars) and the effects of residency and orientation. *Behaviour*, **121**, 20–34.

Miron, G., Desrosiers, G., Retière, C. & Masson, S., 1992b. Variations in time budget of the polychaete *Nereis virens* as a function of density and acclimation after introduction to a new burrow. *Marine Biology*, **114**, 41–48.

Miron, G., Desrosiers, G., Retière, C. & Lambert, R., 1991. Dispersion and prospecting behaviour of the polychaete *Nereis virens* (Sars) as a function of density. *Journal of Experimental Marine Biology and Ecology*, **145**, 65–77.

Miron, G. & Kristensen, E., 1993. Factors influencing the distribution of nereid polychaetes: the sulfide aspect. *Marine Ecology Progress Series*, **93**, 143–153.

Nichols, F.H., 1970. Benthic polychaete assemblages and their relationship to the sediment in Port Madison, Washington. *Marine Biology*, **6**, 48–57.

Olive, P.J.W., 1993. Management of the exploitation of the lugworm *Arenicola marina* and the ragworm *Nereis virens* (Polychaeta) in conservation areas. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **3**, 1–24.

Olive, P.J.W., 1994. Polychaeta as a world resource: a review of patterns of exploitation as sea angling baits and the potential for aquaculture based production. Actes de la 4ème Conférence internationle des Polychètes (ed. J.-C. Dauvin et al.). *Mémoires Muséum d'Histoire Naturel*, **162**, 603–610.

Rasmussen, E., 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia*, **11**, 1–507.

Reish, D.J. & Aloshi, C., 1968. Aggressive behaviour in the polychaetous annelid family Nereidae. *Bulletin of the South California Academy of Sciences*, **67**, 21–28.

Shepherd, P.C.F. & Boates, J.S., 1999. Effects of a commercial baitworm harvest on semipalmated sandpipers and their prey in the Bay of Fundy hemispheric shorebird reserve. *Conservation Biology*, **13**, 347–356.

Snow, D.R. & Marsden, J.R., 1974. Life cycle, weight and possible age distribution in a population of *Nereis virens* (Sars) from New Brunswick. *Journal of Natural History*, **8**, 513–527.

Thomas, N.S., 1987. *Aspects of the ecology of the macroinvertebrates in the intertidal soft sediments of Chichester Harbour.* PhD thesis, University of Portsmouth, Portsmouth, UK.

Thorson, G., 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). *Meddelelser fra Kommissionen for Danmarks Fiskeri-Og Havunder S gelser Serie: Plankton*, **4**, 1–523.

Townshend, D.J. & O'Conner, D.A., 1993. Some effects of disturbance to waterfowl from bait digging and wildfowling at Lindisfarne National Nature Reserve, north-east England. *Wader Bird Study Group*, **68**, 47–52.

Watson, G.J., Bentley, M.G., Gaudron, S.M. & Hardege, J.D., 2003. The role of chemical signals in the spawning of polychaete worms and other marine invertebrates. *Journal of Experimental Marine Biology and Ecology*, **294**, 169–187.

Wieser, W., 1959. The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. *Limnology and Oceanography*, **4**, 181–194.

Williams, M.E. & Bentley, M.G., 2002. Fertilization success in marine invertebrates: the influence of gamete age. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **202**, 34–42.

Submitted 20 June 2006. Accepted 8 January 2007.