

The lugworm fishery in Northumberland, UK: Bait digging impacts in a marine protected area

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ABSTRACT

Robust evidence of fisheries impacts is required to support evidence-based management. Intertidal fisheries have received considerably less attention to date compared to inshore and offshore counterparts. The need for additional intertidal data and assessment has been identified for protected sites under UK legislation (i.e., the Department for Environment, Food & Rural Affairs 'revised approach to commercial fisheries'). Digging for *Arenicola* spp. is carried out both recreationally and commercially within the Berwickshire and North Northumberland Special Area of Conservation (SAC), a Marine Protected Area (MPA) along the northeast coast of England. This study investigated the impacts of such activities, comparing sites across a gradient of fishing pressure (none, low, high), in combination with small scale experimental disturbances (simulated digging and lugworm exclusion) at an unfished site. Fishing pressure gradient studies indicated no long-term impacts on the target species, as no significant differences were detected between sites. This suggests that current collection intensities are not reducing or altering targeted lugworm populations. However, finer scale experimental work revealed significant negative impacts upon the wider sediment communities in the short term, which was mirrored in the longer-term, fisheries scale gradient site comparisons. Reductions in total infaunal abundance and taxonomic richness and altered community structures were observed. Recovery within experimental plots was rapid (within a few months), suggesting that under similar conditions, sites have the potential for substantial recovery if disturbance is ceased. The observed alterations to infaunal communities could have ecosystem wide implications, with altered functional diversity and ecosystem processes that are not compatible with the conservation objectives or designations of the study site. Additional management measures such as further closed areas or seasonal closures to bait digging would allow for recovery and restoring sites.

1. Introduction

Impacts of fishing on marine ecosystems are well recognised and documented globally (e.g. Coleman and Williams, 2002; Collie et al., 2000; Dayton et al., 1995; Kaiser et al., 2006b; Thrush et al., 1998; Williams et al., 2008). However, intertidal activities have received considerably less attention to date. The impacts of all extractive activities need to be understood to realise the global drive for biodiversity conservation and move towards ecosystem-based management (Boonzaier and Pauly, 2016; Levin et al., 2009).

The common lugworm (*Arenicola marina*) and black lugworm (*Arenicola defodiens*) are harvested by bait collectors, an activity which

supports both commercial and recreational fishing, via the supply of fresh bait (they form part of the diet of several targeted demersal fish species) (Cunha et al., 2005; De Cubber et al., 2018). A recent assessment of the global polychaete bait industry estimated that 121,000 t are collected annually, worth £5.9 billion, with *Arenicola defodiens* listed as one of the five most expensive marine species on the global fisheries market (retail price per kg) (Watson et al., 2017a). Lugworms are important ecosystem engineers, structuring the infaunal community via bioturbation processes (Petrowski et al., 2016; Volkenborn et al., 2007; Volkenborn and Reise, 2006; Wright and Jones, 2006).

Despite their ecological importance, and high fishery value, a lack of evidence is available in the UK for the impacts of intertidal collection

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activities on sand and mud flats, highlighted by the Department for Environment, Food & Rural Affairs (DEFRA's) 'revised approach to commercial fisheries' (MMO, 2014) and subsequent evidence scoping assessments. Within Special Protection Areas (SPAs) and Special Areas of Conservation (SACs), fishing activities that are deemed to unfavourably affect conservation features and site integrity are not allowed without putting in place adequate management measures. There is a need for site-specific studies, relative to the local intensity and frequency of a fishing activity, to adequately inform managers whether fishing activities are compatible with the conservation objectives or designated features of Marine Protected Areas (MPAs) (Clarke and Tully, 2014).

Research interests in intertidal fisheries impacts has increased in recent years, resulting in a growing body of literature. Bivalve harvesting within soft sediment intertidal environments has received much attention (e.g. Constantino et al., 2009; Dias et al., 2008; Ferns et al., 2000; García-García et al., 2015), and our knowledge of bait digging for marine worms is not far behind (e.g. Carvalho et al., 2013; Cole et al., 2018; Mosbahi et al., 2015; Watson et al., 2007; Watson et al., 2017b). Within bait digging studies, lugworms are commonly studied in European contexts, with recent focus on large-scale or mechanical harvesting in vast areas such as the Wadden Sea (e.g. Beukema, 1995; van den Heiligenberg, 1987; Volkenborn and Reise, 2007). In the UK, lugworm collection is primarily small scale and carried out by hand with forks or pumps, the effects of which have been historically investigated on the target species populations (Blake, 1979; Howell, 1985; Olive, 1993; Shahid, 1982). Recent evaluations of small-scale lugworm collection across the UK, specifically evidence of the effects on sediment communities, is lacking.

Population structures of targeted lugworm populations can be altered by bait digging, with reduced size and abundance from preferential removal of the largest individuals (Shahid, 1982) and increased mortality (Beukema, 1995; Volkenborn and Reise, 2007). Where impacts are observed, recovery rates are variable, ranging from one month to several years (Beukema, 1995; Blake, 1979; Cryer et al., 1987; Klunder et al., 2021). The physical disturbance of the sediment created by bait diggers can kill or damage infaunal species directly, or indirectly by creating conditions in which the organisms can no longer survive (Chandrasekara and Frid, 1998). Total infaunal biomass is often reduced after digging, with altered community structures due to the varying sensitivities of different species (Brown and Wilson, 1997; van den Heiligenberg, 1987; Watson et al., 2017b). Digging disrupts sediment layering and alters the chemical concentrations in the sediment surface layer (Fowler, 1999; Howell, 1985). Secondary effects from the loss of ecosystem engineers are also a concern (Volkenborn et al., 2007; Volkenborn and Reise, 2006). Recovery rates of infaunal communities after bait digging range from several months up to five years for the most vulnerable species (Beukema, 1995; Fowler, 1999; van den Heiligenberg, 1987).

The present study explored the impacts of lugworm harvesting within a UK MPA – the Berwickshire and North Northumberland Coast Special Areas of Conservation (BNNC SAC). Population size and structure of the target species, *A. marina* and *Arenicola defodiens*, were investigated along with the associated sediment community effects from bait digging. To study direct impacts from known harvesting intensities (FAO, 2005), both comparative and experimental methodologies were combined to observe impacts from actual fishing pressures at appropriate scales (Hughes et al., 2014). Short-term simulated digging and lugworm exclusion experiments at an unfished site allowed changes with disturbance regimes to be monitored, whilst comparisons of discrete shores subject to a gradient of bait digging gave a more holistic view of longer-term impacts under genuine fishery regimes.

2. Materials and methods

2.1. Study area and site selection

The BNNC SAC is a large multi-feature designated site along the coast of northeast England and southeast Scotland. There are several designated and classified features within the area, including mudflats largely within shallow inlets and bays. Within the BNNC SAC, bait digging for lugworms is a sizeable fishery, both recreational and commercial (Tinlin-Mackenzie, 2018), with collection hotspots spread along the coast (Tinlin-Mackenzie et al., 2019), and bait digging byelaws or restrictions present in sections of the site (NCAONB, 2009). Map of the sites in supplementary materials (Fig. S1).

Shores with no, low, and high collection pressure were selected for the comparative study based on shore visits and expert advice (Angling Trust, Natural England, and the Northumberland Inshore Fisheries Conservation Authority), and later confirmed with regular shore observations (estimated harvest weights per year: Lindisfarne National Nature Reserve (LNNR) ~0 kg, Boulmer ~2600 kg, and Newton 500 kg (Tinlin-Mackenzie, 2018; Fig. S2)).

Although some lugworm collection does occur in discrete zones of the LNNR, the site selected for sampling here was several hundred meters away and collection is very minimal overall at LNNR – personal observations). All sites are rural, with no obvious pollution sources, and all classified as 'sand and muddy sand' substrate types (European Nature Information System – EUNIS – classification system), with Boulmer being the muddier of the three sites.

An area of Fenham Flats within the LNNR was selected as the unfished site for the experimental study. This area is protected from bait digging through active enforcement by site managers. The sediment characteristics were classified as 'sand and muddy sand' (EUNIS classification system).

2.2. Comparative study sampling

Sampling was carried out in March 2014, at low spring tides on 3 consecutive days. At each site, ten 1 m² quadrats were spaced randomly along the lower shore, spaced at least 5 m apart (Fowler, 1999). Within each quadrat, *Arenicola* spp. casts were counted and cast diameter measured for five randomly selected casts per quadrat. Number of casts can be used as a proxy for abundance (Flach and Beukema, 1994), and diameter of cast strands for worm size (Retraubun et al., 1996). At these sites, it is mostly *A. marina* present at the shore heights sampled, with *A. defodiens* mostly in the subtidal zone or exposed at extremely low tides, therefore they were not differentiated in the sampling.

To quantify densities of infauna, ten 30 cm deep sediment cores (approx. 4500 cm³ each), next to each quadrat, were collected using a post hole auger. Core samples were not taken to verify cast counts of *Arenicola* spp. (as adults can burrow deeper than the depth to which the core samples were taken), but to characterize the sedimentary community from the surface to a depth of 30 cm. Sediment samples were immediately sieved on site through 0.5 mm mesh sieve bags. Material retained were transferred into screw top plastic bottles with 70% ethanol to cover the samples for preservation. Faunal samples were stained using Rose Bengal solution in 70% ethanol, to distinguish biota from the inorganic material (Tagliapietra and Sigovini, 2010). Samples were rinsed and added to trays containing clean freshwater, and organisms were sorted by eye. Organisms were identified to species level where possible using a compound microscope.

2.3. Experimental study set-up and sampling

At Fenham Flats, sediment disturbance associated with bait digging was simulated within 25 4m² experimental plots, arrayed in a 5 × 5 matrix with 5 m spacing between rows and columns, with wooden posts marking each corner. Each plot was randomly assigned to one of five

treatments: ambient, exclusion, exclusion control, low and high intensity digging. The intensity of sediment disturbance by local collectors was replicated as closely as possible, using a standard 'garden fork' type commonly employed by bait harvesters in northeast England (4 circular tines, handle length 1 m, mass 2150-3800 g). Ambient plots were left untouched. Exclusion plots used 1 mm mesh polyethylene nets, inserted horizontally 10 cm deep into the sediment, to remove lugworms without disturbing the other fauna (a method previously used by: Kuhnert et al., 2010; Volkenborn and Reise, 2006). Exclusion control plots were dug to 10 cm, with no net inserted, controlling for the sediment disturbance caused when inserting an exclusion net. Low digging intensity plots were completely dug over to a minimum depth of 30 cm (the depth observed being used by local collectors at other shores) once every three weeks, and plots backfilled, with no lugworms removed. High digging intensity plots had an increased frequency of once per week for the 10-week study.

Within each plot, *Arenicola* and the infaunal communities were sampled using the same methodologies as described for the comparative study, but with counts conducted within each of the 25 4m² plots rather than quadrats, and three sediment cores collected from inside each plot. All plots were sampled before treatments began, after ten weeks of treatments, and again after recovery period of eleven weeks (Table 1). For the 'exclusion' treatments, infauna were sampled before exclusion nets were in place, and at the ten and eleven week time periods, the corer was allowed to penetrate through the net to the required 30 cm depth. *Arenicola* counts were conducted by counting the casts across the entire plot while infaunal community counts were conducted using the three sediment cores. Changes in sediment surface colouration were noted at each visit, and sediment penetrability was measured in each plot after the treatment period, by measuring the penetration depth (cm) of a garden fork (handle 1 m long, mass 2150 g) dropped from 1 m above the surface (adapted from Johnson et al. (2007)). Recovery sampling occurred for the ambient and simulated digging treatments only, as the exclusion treatments required the removal of nets, which would have introduced new disturbance.

2.4. Data analysis

Fishing pressure on the target species (*Arenicola*) density, size, and diversity (Shannon Weiner function) were analysed using R version 4.0.4 (R Core Team, 2021). The differences between sites, treatments and times were tested using linear models and one-way ANOVAs where parametric assumptions were met, along with Kruskal-Wallis tests (Dytham, 2011; Underwood, 1997). Subsequent Tukey pairwise comparisons were made where necessary for ANOVA. All Post hoc tests were performed using the base stats package in R (R Core Team, 2021).

Infaunal community composition was analysed using multivariate methods (ANOSIM, permutations = 9999) in R using the vegan package (Oksanen et al., 2020) and linear mixed effect models (LMEs) (Pinheiro et al., 2021). The LMEs included quadrats nested in treatment and time as a random effect to capture any variation in the data that resulted from experimental design. Bray Curtis similarity was calculated on square root transformed averaged data, with results expressed in non-metric multidimensional scaling plots (nMDS). SIMPER analysis was used to determine the species responsible for the differences observed.

Table 1

Sampling scheme – survey dates for each treatment in each sampling period.

	Before	After	Recovery
Ambient	18th April 2014	28th June	13th September
Exclusion	18th April 2014	28th June	N/A
Exclusion Control	18th April 2014	28th June	N/A
Low Digging	18th April 2014	28th June	13th September
High Digging	18th April 2014	28th June	13th September

3. Results

3.1. Fishing pressure site comparisons

3.1.1. Target species

Densities of *Arenicola* spp. based on cast sampling were significantly different between sites (ANOVA, $F = 8.079$, $df = 2, 27$, $P < 0.01$). Post hoc Tukey pairwise comparison revealed lugworm density was significantly lower at LNNR, the site with no harvesting, (mean = 13.4 ± 5.27 SD), compared to Newton, whilst Boulmer and Newton had statistically similar densities ($p > 0.05$) (Fig. 1). The median cast diameters did not differ statistically between sites (Kruskal-Wallis, $H = 1.32$, $df = 2$, $P > 0.5$) (Boulmer: med = 3, min = 1, max 5; Newton: med = 4, min = 1, max = 5; LNNR: med = 3.5, min = 2, max = 6) (Fig. 2).

3.1.2. Infaunal community

Annelids dominate at all three sites, with crustaceans also occurring in high numbers (Table S1). The three most abundant taxa recorded were: *Notomastus latericeus*, *Tubificoides* sp., and *Urothoe poseidonis*. Both *N. latericeus* and *Tubificoides* were only present in high numbers at LNNR, whilst *U. poseidonis* were much more abundant at Newton. Taxonomic richness was significantly different between sites (ANOVA, $F = 3.53$, $df = 2, 26$, $P < 0.05$). A Post hoc Tukey pairwise comparison revealed that LNNR had the highest taxonomic richness, whilst the lowest occurred at Newton (Table 2). The median infaunal abundances were significantly different between sites (Kruskal-Wallis, $H = 6.40$, $df = 2$, $P < 0.05$). Boulmer, the heavy harvesting site, had considerably lower average infaunal abundance (median = 20.0 ± 33.0 range), the median abundance being less than half that of the other sites. Diversity also was significantly different between sites (ANOVA, $F = 3.89$, $df = 2, 26$, $p < 0.05$), being lowest at Newton.

Community structure of the infaunal organisms was significantly different between sites (ANOSIM: Permutations = 9999, Global $R = 0.8776$, $p < 0.001$). Bray Curtis similarity revealed that all sites have a comparable similarity level at around 40%, with good discrimination between communities from each site (Fig. 3). The two harvested sites were more similar than the site with no harvesting. SIMPER analysis

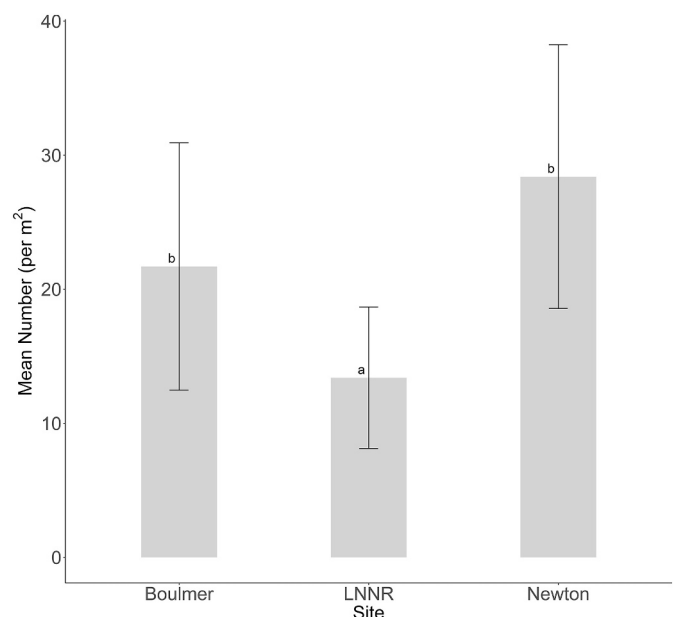


Fig. 1. Mean (\pm SD) number of lugworms per m² (Boulmer = heavy harvesting, Newton = light harvesting, LNNR = no harvesting), sampled March 2014, using quadrats (1m²) to count casts on the surface; $n = 10$ for all sites. The sites are labelled according to the results of the Tukey test LNNR (a) being different to the other two sites (b).

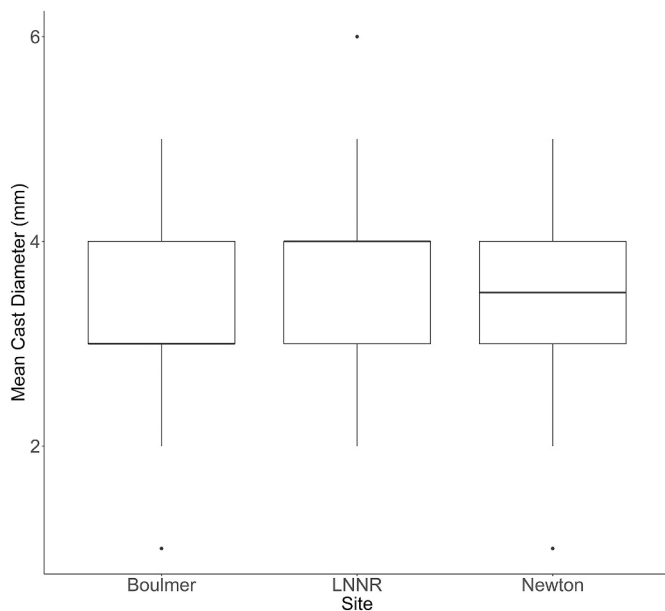


Fig. 2. A box and whisker plot of cast diameters (mm) of lugworms (Boulmer = high collection pressure, Newton = light harvesting, LNNR = no harvesting), showing the Q1, Q2, Q3 and the upper and lower fences. The dots represent outliers in the data not captured by the fences. Samples were taken in March 2014, with 5 casts measured from 10 1m² quadrats; n = 50.

Table 2

Median (± range) infaunal abundance, mean (± SD) taxonomic richness, and Shannon’s diversity for each site (Boulmer = heavy harvesting, Newton = light harvesting, LNNR = no harvesting), sampled March 2014 (n = 10, sediment volume = 4500 cm³ each).

	Boulmer	Newton	LNNR
Abundance	20.0 (± 33.0)	42.5 (± 54.0)	49.0 (± 77.0)
Taxonomic richness	9.0 (± 2.92)	7.9 (± 2.60)	11.4 (± 3.43)
Diversity	1.8 (± 0.39)	1.4 (± 0.23)	1.8 (± 0.33)

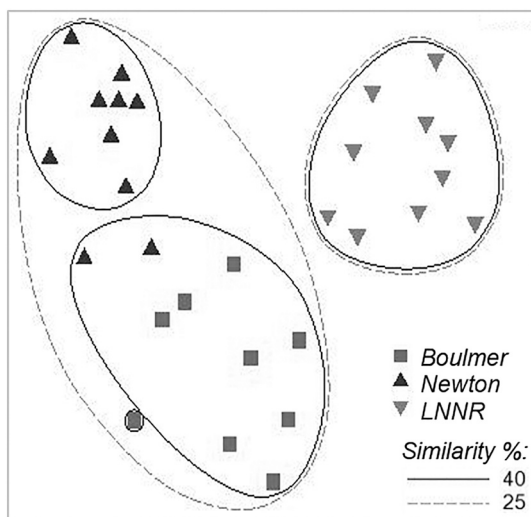


Fig. 3. nMDS ordination of the Bray Curtis similarity based on square root-transformed averaged abundance data (Boulmer = heavy harvesting, Newton = light harvesting, LNNR = no harvesting), sampled March 2014. 2D Stress: 0.12. Overlays of Bray Curtis similarity groupings at 25 and 40%.

shows that the main taxa responsible for the differences are: *Urothoe poseidonis*, *Tubificoides* sp., *Spio martinensis*, and *Notomastus latericeus*, which are also some of the most dominant species recorded. LNNR contained the vast majority of *N. latericeus* and *Tubificoides* sp. specimens, whilst *U. poseidonis* and *S. martinensis* were most abundant at Newton (Fig. 4).

3.2. Simulated digging and exclusion experiments

3.2.1. Target species

Lugworm density was significantly different between treatments (ANOVA, $F = 9.168$, $df = 4, 58$, $P < 0.001$). Post hoc Tukey pairwise comparison ($p < 0.01$) showed that lugworm density was significantly lower for both the high and low digging intensities when compared to the ambient plots (Fig. 5). Lugworm density was also significantly different between treatment periods (ANOVA, $F = 25.689$, $df = 2, 58$, $p < 0.001$). Post hoc Tukey pairwise comparison showed lugworm density was significantly different in both the after ($p < 0.001$) and recovery ($p < 0.001$) periods than before the treatments. Lugworm density was not significantly different ($p > 0.05$) between the after and recovery periods. A more descriptive breakdown of the relationships between treatment and digging treatment can be seen in the supplementary materials (Table S2). Exclusion plots only reduced the mean density to 65% of ambient levels. High digging intensity plots had the lowest density, with just 13% of the ambient levels, despite no worms being removed during treatments. After the recovery period, lugworm density remained significantly different between treatments (ANOVA, $F = 15.37$, $df = 2, 62$, $P < 0.01$), being significantly lower in the high digging intensity plots (mean = 21.94 ± 10.97 SD) compared to ambient conditions (mean = 28.12 ± 14.06 SD) (Fig. 5).

3.2.2. Infaunal community

The two most abundant taxa recorded were Nematoda, and *Pygospio elegans*, both of which decreased in abundance with the presence of digging, with *P. elegans* reduced to just 4% of ambient levels in the high digging plots (Table S3 in supplementary materials).

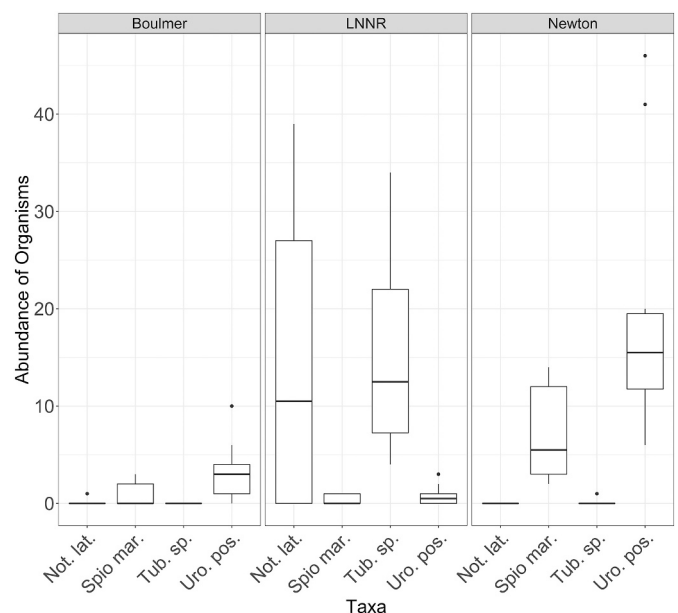


Fig. 4. A box and whisker plot showing the abundances of the four species most responsible for the difference in community structure describing the Q1, Q2, Q3 and the upper and lower fences. The dots represent outliers in the data not captured by the fences. (Boulmer = heavy harvesting, Newton = light harvesting, LNNR = no harvesting), sampled March 2014 (n = 10 sediment samples each 4500 cm³).

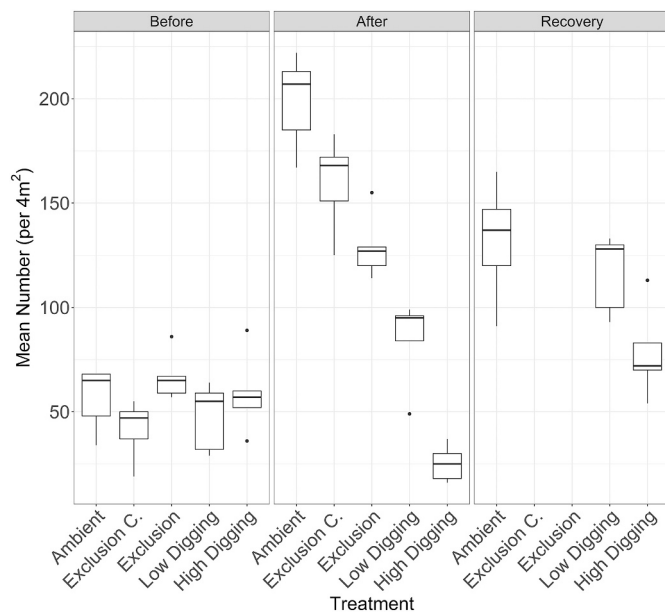


Fig. 5. A box and whisker plot showing the number of lugworms per plot (4m²) across each treatment (ambient, exclusion control, exclusion, low digging intensity, and high digging intensity), describing the Q1, Q2, Q3 and the upper and lower fences. The dots represent outliers in the data not captured by the fences. Samples were taken before the treatment (April 2014), 10 weeks after the treatment (June 2014), and after 11-week recovery period (September 2014) by surface cast counts; n = 5 for all treatments.

The taxonomic richness was significantly different in the high digging treatment (Table 3). Richness was reduced in the exclusion, low digging, and high digging plots but only significantly in high digging plots. The amount of variation explained by the random effects (period and quadrat) was approximately 19% suggesting the random effects did not have a huge impact on species richness. Infaunal abundance was also affected by treatment (Table 3) with only the high simulated digging treatments being significantly different from ambient. The random effects explained 34% of variation in the infaunal abundance. Lastly, Shannon’s diversity was not significantly affected by the presence of disturbance, so the results were omitted.

Community structure also differed between treatments. Bray Curtis similarity shows good discrimination between treatments after the treatment period only, with high digging distinct from the other treatments (Fig. 6). ANOSIM (9999 permutations) revealed that community assemblages were statistically different between all treatments after the treatment period ($R = 0.165$; $p < 0.001$). SIMPER analysis revealed the taxa that contributed most to the differences before and after treatments in the high digging plots were: *Pygospio elegans*, Nematoda, and *Tubificoides* sp. which were also dominant (Fig. 7). The reductions for

Table 3
Results from linear mixed effect models comparing the species richness and abundance between treatments from the before and after treatment periods.

Measure	Treatment	Mean	Std Error	DF	t-value	p-value
Species Richness	Exclusion	-1.566	0.885	20	-1.77	0.092
	Exclusion Control	0.066	0.885	20	0.08	0.941
Abundance	Low Digging	-2.900	0.885	20	-1.81	0.086
	High Digging	-1.600	0.885	20	-3.28	<0.01
	Exclusion	0.466	11.30	20	0.04	0.968
	Exclusion Control	3.166	11.30	20	0.28	0.782
	Control					
	Low Digging	-22.83	11.30	20	-2.02	0.057
	High Digging	-37.26	11.30	20	-3.30	<0.01

P. elegans (Value = -23.6, std. error = 3.828, df = 24, $t = -6.17$, $p < 0.001$, random effects = 43%) and *Tubificoides* sp. (Value = -2.07, std. error = 0.733, df = 24, $t = -2.82$, $p < 0.01$, random effects $\leq 1\%$) were significant, whilst Nematoda (Value = -1.4, std. error = 2.12, df = 24, -0.66 , $p > 0.5$, random effects $\leq 1\%$) was statistically similar. After the disturbance period, 82% of taxa were reduced, with the dominant taxonomic group altered from Annelids to Nematoda.

The infaunal community recovered well, with mean abundances shown in Fig. 8 for the three sample periods. Differences were no longer significant after the recovery period (Low Digging: $p > 0.5$, High Digging: $p > 0.9$). The mean taxonomic richness was also similar between treatments after the recovery period, with the high digging intensity plots having the highest average richness. Community structure also recovered; ANOSIM (9999 permutations) reveals that community assemblages were no longer statistically different between treatments ($R = 0.044$; $p > 0.05$), with high Bray Curtis similarity values and little distinction between groups (Fig. 6).

3.2.3. Habitat alterations

Sediment characteristics were noticeably altered during treatments. Simulated digging plots were darker from the redistribution of anoxic sediment to the surface, with changes persisting until the next disturbance. Sediment penetrability and softness was altered by digging, with fork penetration depths being significantly different between treatments (Kruskal-Wallis, $H = 55.07$, df = 4, $P < 0.001$, Fig. 9), increasing with the presence of digging. A Pearson’s correlation test revealed that the density of lugworms was significantly correlated (-0.46 , $p < 0.001$) with sediment penetrability.

4. Discussion

The dual approach of combining experimental with comparative studies that integrate both short- and long-term observations offers a unique perspective into the impacts of baitworm digging. In the short-term, both lugworm and infaunal abundance was markedly reduced by the digging, the severity of such impacts linked to the intensity of collection. In the long-term, lugworm populations are maintained. There is no evidence of reduced abundance or size at heavily collected sites, with populations sustained at harvestable levels. Negative secondary impacts on the infaunal communities persisted in the long term at fished sites; however, the

recovery of the infaunal community in the experimental plots was rapid, likely from surrounding, unimpacted communities in the sediment. This suggests that recovery elsewhere is possible if sufficient and well-timed no-take periods, or closed areas, were to occur. Managers must consider whether the level of impact observed is important at the SAC scale, which is discussed below.

4.1. Impacts upon the target species

The contrasting findings on the target species seen here further highlights the importance of scale in impact studies, both spatially and temporally (Reise et al., 2001; Thrush et al., 1996; Watson et al., 2017b). Small scale, short-term experiments are important to study direct impacts, without interference from natural and anthropogenic derived variability between sites in a comparative study, whilst comparative studies offer insight into the long-term real-world effects over larger spatial scales, allowing for factors such as recruitment. In the comparative site study, neither lugworm density nor size appear to be negatively correlated to long-term bait digging pressures at current exploitation levels. In contrast, short-term impacts were observed in disturbance experiments, with significantly reduced lugworm abundance recorded in the simulated digging plots.

Lugworm densities can vary considerably between locations, being dependent on environmental factors such as food availability or sediment characteristics (Cadée, 1976; Callame, 1961; Longbottom, 1970),

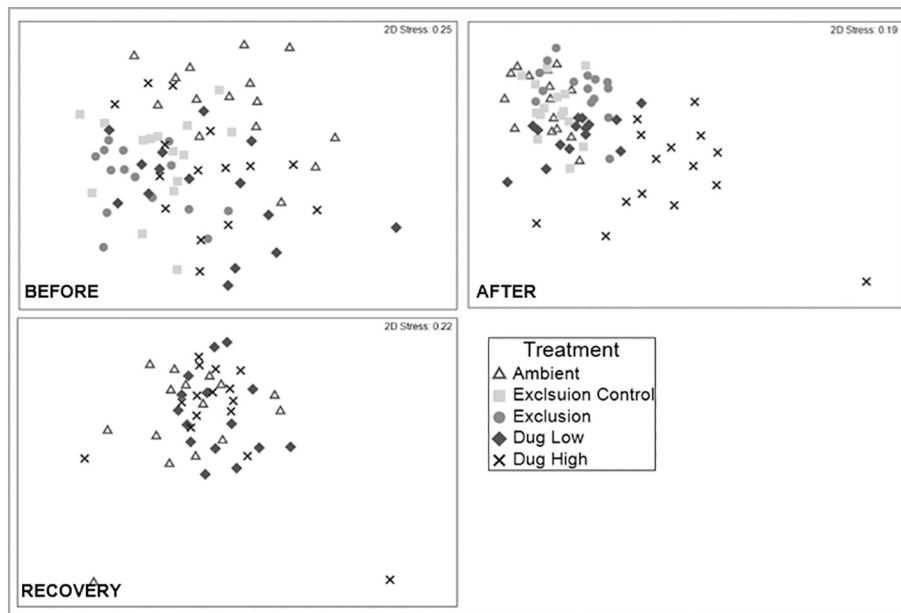


Fig. 6. nMDS ordination of the Bray Curtis similarity based on square root-transformed averaged abundance data per treatment (ambient, exclusion control, exclusion, low digging intensity, and high digging intensity), before and after the 10-week treatment period, and after the 11-week recovery period. Sampled April, June, and September 2014, respectively.

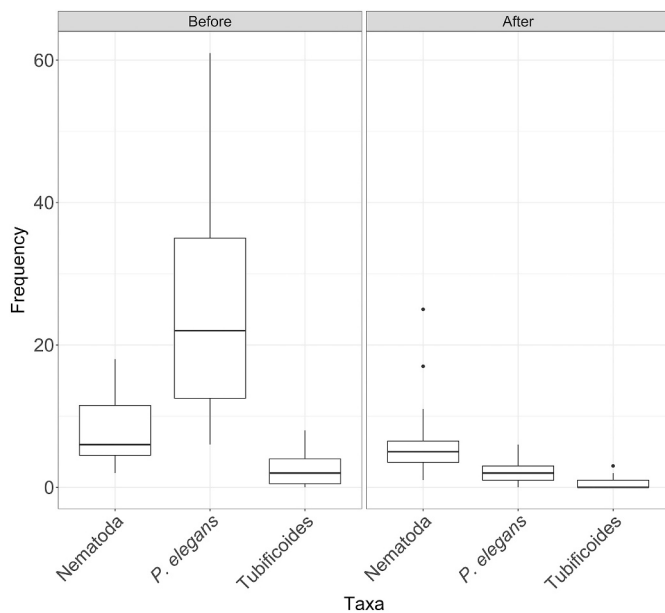


Fig. 7. A box and whisker plot showing the number (per 4500 cm³) of the three taxa selected from SIMPER analysis per treatment (ambient, exclusion control, exclusion, low digging intensity, and high digging intensity), before and after 10 weeks of treatment. Sampled April and June 2014 and (n = 15). The plot describes the Q1, Q2, Q3 and the upper and lower fences. The dots represent outliers in the data not captured by the fences.

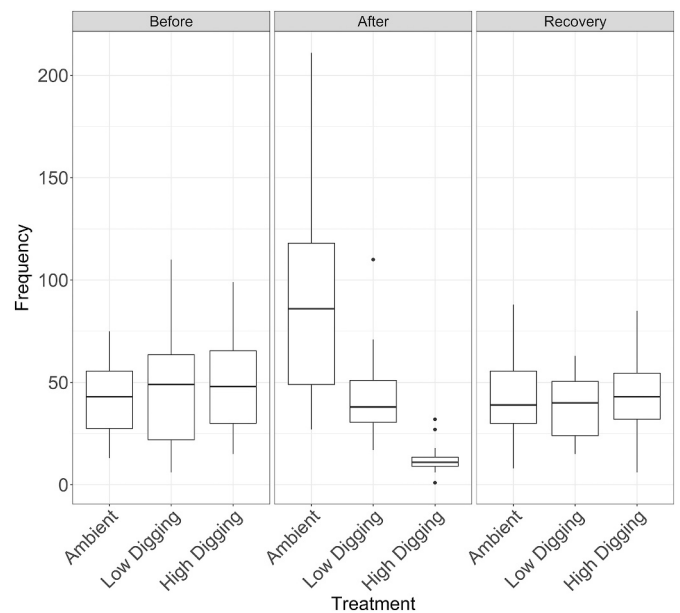


Fig. 8. A box and whisker plot showing the number of organisms (in 4500 cm³) for each treatment (ambient, low digging intensity, and high digging intensity) before the simulated disturbance began, after 10 weeks of disturbance, and after a recovery period of 11 weeks. n = 15 per treatment. The plot describes the Q1, Q2, Q3 and the upper and lower fences. The dots represent outliers in the data not captured by the fences.

and affected by anthropogenic factors such as trampling and pollution (Browne et al., 2013; Rossi et al., 2007). Differences other than collection pressure between the comparative sites (e.g., small sediment differences, environmental and chemical variances, and other anthropogenic inputs), which were not measured here, are important to acknowledge, and could be capable of masking impacts of harvesting on lugworm populations. In addition, fishers' choice is capable of complicating the observations further, as bait diggers preferentially target shores with naturally higher abundances of lugworm (Tinlin-Mackenzie,

2018). However, there is anecdotal evidence that bait digging has occurred intensely at Boulmer for many years, yet it still maintains abundant lugworm populations. In the experimental study, untouched patches of sediment surrounding small experimental plots may have resulted in surviving lugworms migrating out of disturbed plots into more suitable habitat (e.g. lower penetrability, higher oxygen contact and organic matter (Longbottom, 1970)), giving the impression of reduced densities at the small scale. This refuge area would not be available at fished sites and could explain the maintained densities

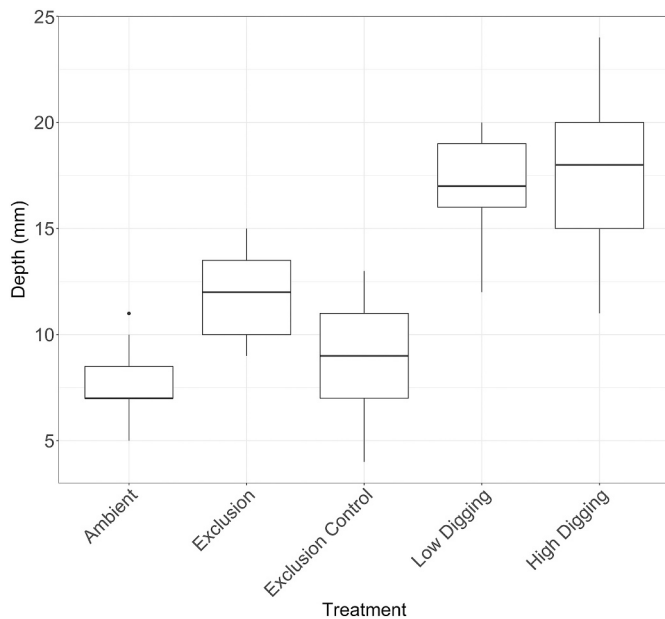


Fig. 9. A box and whisker plot showing the sediment penetration (mm) in each treatment after the treatment period (10 weeks) (ambient, low digging intensity, and high digging intensity) describing the Q1, Q2, Q3 and the upper and lower fences. The dot represents outliers in the data not captured by the fences.

observed in the longer term.

Previous studies have revealed reduced lugworm abundance due to harvesting, however these studies generally had a higher harvesting intensity than that identified here, with either targeted simulated digging or mechanical harvesting (Beukema, 1995; Volkenborn and Reise, 2007). Shahid (1982) found no change in lugworm abundance with the presence of bait collection, but did record a reduction in size. Despite long-term, high-intensity harvesting, lugworm density at Boulmer has remained relatively high along with large average worm size suggesting little impact on the target species. This maintenance is likely due to the worm's ability to recolonise rapidly, long lifespan, inverse relationship between recruitment rates and adult density, high dispersive potential of larvae, and high fecundity related to self-recruitment (Beukema and De Vlas, 1979; Günther, 1992; Olive, 1993; Swearer et al., 2002). Recruitment from surrounding undisturbed areas within both elsewhere within the SAC, and immediately adjacent in the no-take area, may be helping to keep exploited populations stable in the long term. Anecdotal reports have suggested reduced density at Boulmer over time. In the absence of historical lugworm data to assess changes over time, such claims cannot be investigated further unless ongoing monitoring data is established to observe ongoing changes. But the detectable impacts at the unfished, experimental disturbance site provide some insight into the short-term, direct impacts of bait collection on a baseline site.

Overall, lugworm harvesting at current intensities within the SAC does not appear to result in long term discernible impacts on the target species over natural variability. Short-term impacts appear to stabilise over longer timescales and larger spatial scales, with exploited populations remaining at harvestable levels for some time. There is no direct evidence of reduced lugworm populations, and as such lugworm harvesting within the BNNC SAC appears to not significantly impact upon the target species at the current exploitation rates (Tinlin-Mackenzie, 2018).

4.2. Impacts upon the sediment community

Negative impacts upon the infaunal sediment communities were evident in both the comparative and experimental studies, suggesting

impacts implemented in the short-term Fenham Flats study are sustained in realistic bait digging regimes. The significant reductions in infaunal abundance that occurred at the highest digging intensity during the experimental periods, were similarly observed in previous studies, where a 40% reduction in biomass has been reported (van den Heiligenberg, 1987). A major conservation concern with reduced abundance or biomass is the food web implications, with potential negative consequences for infaunal-feeding birds, particularly those species with strong prey preferences (Bowgen et al., 2015; Masero et al., 2008; van den Heiligenberg, 1987). Migratory birds are especially vulnerable to prey decline, relying on a few specific coastal areas during their journey (Masero et al., 2008; Skagen and Knopf, 1993). The boundary of the BNNC SAC also contains multiple SPA designations that are key sites for the protection of important bird populations (NCAONB, 2009); however, none of the highest intensity bait digging sites within the SAC are currently within SPA boundaries (Tinlin-Mackenzie et al., 2019), and some supporting mud habitats are protected from activities such as bait digging, suggesting that some alternative feeding grounds remain unimpacted.

Community structure was directly altered in experimental plots after 10 weeks, with reduced taxonomic richness, and a shift in dominance from Annelids to Nematodes. Communities were also significantly different between comparative sites. Heterogeneity of infaunal community structure along a coastline is well documented (e.g. Morrissey et al., 1992; Norén and Lindgarth, 2005), with a variety of influencing factors such as habitat, environmental conditions, contamination, fishing activities, or a combination (e.g. Beukema, 1976; Kaiser et al., 2001; Ruso et al., 2007; Stark et al., 2005; Van Hoey et al., 2004). The habitat and environmental conditions at Boulmer, being muddier with higher organic content, should lead to a highly abundant and diverse community under natural conditions, but also one less resilient to disturbance than more mobile sandier sites (Ferns et al., 2000; Kaiser et al., 2006a; Roberts et al., 2010). This increased vulnerability related to sediment type may influence and exaggerate the impact of bait digging here. There may be other confounding factors which varied between the comparative shores which were beyond the scope of this study, such as currents, fetch, etc., that may have also contributed to the community differences observed here.

Some species are more vulnerable to sediment disturbance than others (e.g. Chandrasekara and Frid, 1998; Jackson and James, 1979), resulting in altered communities as opportunistic species increase, and sensitive species decline (Beukema, 1995; Reise, 2001). Nematodes were among the few taxa that did not decline in the experimental plots, similar to the findings of other studies (Watson et al., 2017b). Nematodes are thought to be more resilient to physical disturbance than larger organisms because they are less likely to be killed by the disturbance, have a relatively high tolerance to low oxygen levels, and fast recovery rates (Schmidt-Rhaesa, 2014). However, Nematode communities, being very small organisms, are not always fully represented 0.5 mm sieves, and so these findings should be taken with caution under these sampling methods. *Tubificoides* spp. was significantly reduced in the high digging treatments at the experimental site and was rare or absent at the two collected comparative sites. *Tubificoides* spp. have limited mobility and as a result has been referred to as 'vulnerable', especially to sediment deposition (Genis Trait Handbook, 2015), suggesting that digging disturbances could be responsible for the reduced abundances at bait digging sites, with similar negative impacts observed from bait digging the Solent (Watson et al., 2017b). Recolonisation of Tubificid populations are slower than other similar opportunistic species due to life traits such as prolonged reproductive periods, internal fertilisation, and long lifespan (Tillin, 2018). Changes in communities like these raise concerns for altered functional diversity and ecosystem functioning and processes (Diaz and Cabido, 2001; Solan et al., 2004). Further research into functional trait effects of bait digging is needed to investigate wider reaching consequences on the ecosystem.

Within the community shifts observed in the experimental treatment

periods, it is important to acknowledge the role of seasonality. The treatments occurred over two seasons, beginning in Spring (April) and ending in June (Summer), with recovery sampling in late Summer (September). Over spring and summer, many species have their most active and reproductive season (Beukema, 1974), and so natural abundance and community structure fluctuations are to be expected during this time (Klunder et al., 2021). However, the inclusion of the ambient plots for comparison in this experimental design allows the natural seasonality to be observed, and the differences from this to the other treatments to be related. For example, the average abundance increased between April and June within control plots, likely do to natural seasonal effects, whereas the digging plots saw a significant decrease in this time, suggesting that the negative impacts of bait digging far outweighed the background seasonal effects.

The reduction in lugworm density in exclusion plots to 65% revealed that even marginally reduced lugworm populations can have significant detrimental impacts on the associated sediment community, with lower taxonomic richness observed in exclusion plots. Lugworms are habitat engineers, mixing and reworking the sediment, their burrows transporting oxygen and forming microhabitats, ultimately playing an important role in structuring benthic communities (e.g. Brey, 1991; Reise, 2002; Retraubun et al., 1996; Volkenborn et al., 2007). Removing lugworms from a shore can result in substantial indirect impacts, with different species either positively or negatively affected (Petrowski et al., 2016; Sousa et al., 2017; Volkenborn and Reise, 2007). This study is the first to demonstrate that even slightly reduced lugworm abundance, a much more realistic scenario from lugworm overexploitation than local extinction (van den Heiligenberg, 1987), can have detrimental community scale impacts.

Recovery rate of infaunal communities is dependent on many factors, such as season, scale of disturbance, sediment characteristics, community structure, and the method of recolonization (e.g. Beukema, 1995; Dornie et al., 2003; Klunder et al., 2021; Reise et al., 2001; Zajac and Whitlatch, 1982). As such, there is high variability in the recovery rates observed between previous bait digging studies, ranging from one month to 3 years for the target species (Beukema, 1995; Blake, 1979; Cryer et al., 1987), and 140 days to 5 years for infaunal communities (Beukema, 1995; van den Heiligenberg, 1987). The infaunal community recovered very fast in experimental plots here, in under 80 days. Experimental factors in favour of recovery included the summer timing, the small spatial and temporal scale of disturbance, close proximity of refuge areas from which recolonisation was possible, and the lack of large and delicate species in the area (Beukema, 1995; Brown and Wilson, 1997; Ford et al., 1999; Klunder et al., 2021; Reise et al., 2001). In fished sites such as Boulmer, conditions for recovery are less favourable, due to digging occurring year round (Tinlin-Mackenzie, 2018), with very little undisturbed time for recovery to take place or source of infaunal recruits in close proximity. Other less intensively fished areas within the SAC may have better recovery conditions due both lower intensity harvesting, and the presence of periods of low or negligible activity outside of the peak winter sea angling season (Tinlin-Mackenzie, 2018), and should be assessed on a case-by-case basis. This is especially true for recoverability outside of the spring-summer season investigated here in the experimental plots, as recovery rates are thought to be closely linked to the spring-summer activity of the infaunal species present (Klunder et al., 2021).

Overall, there are significant negative impacts on the infaunal communities associated with bait digging. Both abundance and community structure are altered in the short term (during experimental treatments, but only significantly so at the highest experimental digging intensity) and mirrored in the long term (at comparative sites). Knock-on impacts on higher food web levels, as well as ecosystem functioning, needs further investigation, as well as management considerations to boost recovery. Whilst lugworm populations appear robust to the level of harvesting in the sites studied, the results demonstrate that there are impacts on the larger faunal community, and potentially affect

the resistance and resilience of infaunal communities to disturbance, further highlighting the need to have areas which remain largely undisturbed, to provide sources of recruits, and “spawner sanctuary” areas for adults to breed.

5. Conclusions and management implications

This study provides two separate evidence bases, which are compared and contrasted, to illuminate direct short-term and more realistic long-term impacts of lugworm collection activities. In addition, it provides valuable baseline information to help inform local management plans for the BNNC SAC and other protected areas within the UK.

Findings suggest that impacts of digging on lugworms at the intensities used here are not discernible against natural background variability, and that at current, local collection levels, lugworm collection appears to have low-negligible impact at the target species level, with stable lugworm communities maintained throughout the study area. In contrast, substantial negative impacts exist at the level of the infaunal community in the short term (experimental) that appears to be mirrored at fished sites with high intensity digging (comparative). This is a key sub-feature of the BNNC SAC (European Union Council Directive. 92/43EEC, 1992), and as such should be protected.

High spatial selectivity of diggers within the SAC is important to note, as it results in isolated patches of high intensity collection along the coast (Tinlin-Mackenzie et al., 2019). This leaves other areas of shore unimpacted by bait digging activities. Managers should consider whether the small areas impacted are severe enough to be a significant issue at the SAC scale. Management considerations could focus on reducing impact or increasing recovery. Impact could be reduced by promoting less destructive harvesting methods such as bait pumping which is capable of collecting *A. defodiens* only. This method creates less sediment disturbance and does not produce spoil heaps responsible for smothering small, slow-moving or immobile infauna (Fowler, 1999). Unfortunately, populations of *A. defodiens* are much scarcer than *A. marina* within the region (Tinlin-Mackenzie et al., 2019), which would limit the effectiveness of the proposed action. Barriers to recovery could be removed by management measures, such as closed zones creating refuge areas, closed seasons during spring or summer to maximise recruitment success, or maximum size limits based on fecundity data. The importance of continued monitoring is highlighted, as it is possible that cumulative impacts over longer timescales may differ, especially if harvesting intensity increases in the future.

CRedit authorship contribution statement

Ashleigh Tinlin-Mackenzie: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Ben W. Rowland:** Writing – review & editing, Formal analysis. **Jane Delany:** Resources, Supervision, Writing – review & editing. **Catherine L. Scott:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing. **Clare Fitzsimmons:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

Declaration of Competing Interest

none.

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Appendix A. Supplementary data

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