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RESEARCH ARTICLE OPEN ACCESS

Experimental estimation of ladder dredge efficiency for capture of European flat oysters over mixed sediment

Tom C. Cameron[1,*], Russell Smart[1], Alice Lown[1], Alex Baker[2] and Rebecca Korda[2,3]

[1] School of Life Sciences, University of Essex, Wivenhoe Park, Colchester, CO43SQ, UK
[2] Natural England, County Hall, Spetchley Road, Worcester, WR52NP, UK
[3] Present address: Marine Management Organisation, Lancaster House, Hampshire Court, Newcastle upon Tyne NE47YH, UK

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Abstract – Fishing gear-based landings or survey methods are often used to make assessments of species stock abundance. In order to convert catch into abundance values, estimates or assumptions are made on the catch efficiency of the gear-based method. This is the case in areas where flat oysters, *Ostrea edulis*, are surveyed for fisheries and conservation objectives in a range of projects across Europe. Flat oyster dredge efficiency assumptions vary widely from 5–30% in published studies and uncertainty in what is an appropriate efficiency estimate has led some survey teams to switch to Catch-per-unit-effort (CPUE), where CPUE is also of concern should catch efficiency change with shellfish density, ground type or some other unmeasured variable such as shellfish distribution. We undertook an experimental approach to estimate dredge efficiency in a standard ladder dredge used to harvest and survey adult flat oysters in the UK and Ireland. The dredge efficiency trials assessed how efficiency was influenced by oyster density (between 1 and 2.2 oysters m^2), distribution (clumped vs uniform) and ground types across a gradient of more hard to more soft surface sediments. Dredge efficiency was significantly affected by oyster distribution, but also density and ground hardness as well as their interactions. While a median value between 7 and 10% seems an appropriate universal ladder dredge efficiency to adopt, ground type and distribution had such an effect that local conditions may effect this considerably. Catch efficiency was negatively density-dependent, this makes CPUE methods challenging where oyster densities are likely to vary. Practitioners, regulators and researchers conducting surveys can improve CPUE approaches through standard techniques and knowledge of how catch efficiency varies as we have presented here.

Keywords: Oyster / catch-per-unit-effort / dredge efficiency / Fisheries / uncertainty / density-dependence

1 Introduction

Understanding the relationship between population abundance, sampling effort and catchability has been a long-standing knowledge gap in fisheries management (Powell, Ashton-Alcox and Kraeuter, 2007; Walker *et al.*, 2017). If the relationships between fishing effort, gear type, catch and population abundance are known, this reduces uncertainty in any estimate of population abundance that can contribute to the sustainable management of natural resources by setting appropriate quota on effort or landings.

In shellfisheries, fishing gear-based methods are often used to assess what the likely area based density or population abundances are yearly, or prior to setting of quota or opening of any fishery. While alternative fishing independent assessments are sought, such as low tide cockle surveys for example, they are not always possible or feasible for all fisheries. An example of this is in fishing for whelks that are caught using baited traps both commercially and for assessment (Morel and Bossy, 2004). For some bivalve shellfish, if they are exposed at low tide then condition, density, aerial extent and distributions can be examined with ease, e.g. Exe estuary mussel stock assessment by Devon & Cornwall Inshore Fisheries and Conservation Authority (Curtin, 2022). In species that live sub-tidally whether in or on the sediment this is not always possible, and in many scenarios water turbidity in inshore tidal systems prevents video or diving as survey alternatives (e.g. Bergstrom *et al.*, 2021; Thorngren *et al.*, 2019). This is the case for the European or 'Flat' oyster (*Ostrea edulis*) in several southern North Sea sites.

Flat oysters are most often caught by sail or engine powered ladder dredging, so use of a grabbing method in known areas represents an appropriate fishery independent alternative to assess density (Mann *et al.*, 2004; Schulte,

*Corresponding author: tcameron@essex.ac.uk

Lipcius and Burke, 2018; Allison, 2019). However, a grabbing effort to gain ratio means that this method may only be appropriate in areas of known higher density. Even what are considered large grabs, used by most inshore research vessels (e.g. 0.1–0.2 m^2 van Veen or Day grab), can struggle to detect oysters in the expansive areas of low oyster density that this species is now renowned for (reviewed in Cameron, 2022). Notably, when grabs were last recommended for fishery assessment of subtidal oysters, the densities the researchers were experiencing were 1.5–5 oysters m^2 compared to 0.1–0.5 m^2 being common densities today (Key and Davison, 1981).

Given the range of limitations on sampling methods for subtidal shellfish population assessment, statutory authorities have tended to use fixed transect or point dredge tows using a similar dredge that would be used in the fishery. In the context of flat oysters this is what is known as a ladder dredge and is reported as the main survey dredge used in flat oyster assessments by Inshore Fisheries and Conservation Authorities (KEIFCA) responsible for the North Essex, Thames and Kent oyster populations (Dyer, 2019). Statutory surveys in the Solent, the Fal in Cornwall (reviewed in Cameron, 2022), the Loughs Agency in Northern Ireland and also others internationally use similar ladder dredges (Loughs Agency, 2020). It is therefore also the methods used for estimates of the population size and biomass of flat oysters in the Blackwater Crouch Roach and Colne Marine Conservation Zone (BCRC MCZ) for designation (Allison *et al.*, 2020), subsequent management byelaws and estimation of any baselines and trends for recovery (Lown *et al.*, 2020).

Despite the wide use of dredge assessments for oysters by different IFCA regions, as well as by a range of restoration projects and research organisations, it has been noted that an equally wide range of dredge efficiency assumptions are made in order to estimate the likely oyster abundance or density on the seabed (Cameron, 2022). For example in 2017 a 5% ladder dredge efficiency was used and justified so as "not to underestimate density estimates" (SIFCA, 2017). Later this approach was abandoned due to efficiency uncertainty and Catch per Unit Effort (CPUE) was used instead (SIFCA, 2019). Likewise other regional IFCAs make their own justification for a dredge efficiency value to apply to catches. Having previously used a value of 25% for all oysters, the Northern Ireland Loughs agency uses a value of 25% for larger adult oysters but 12.5% for smaller 1 year olds and 5% for spat based on baseline surveys conducted by CEFAS in 2006 (Loughs Agency, 2020). In the original submission to DEFRA to support the designation of the BCRC MCZ the Essex Wildlife Trust and the University of Essex used a value of 10%, but this was later dropped due to uncertainty and instead catch per dredge reported in future work (e.g. CPUE, Allison *et al.*, 2021). Later a literature review determined that a dredge efficiency value of 20% may be the most likely median value (KEIFCA, 2016). This review was revisited and a range of values from 10 to 30% was considered reasonable for BCRC MCZ assessments (Lown, 2019).

Dredge efficiency assumptions are important in fisheries management and also particularly important in assessment of wild oysters in poor, declining or improving condition as baselines for restoration are vitally important (Mann *et al.*, 2004; Marenghi *et al.*, 2017; Powell, Ashton-Alcox and Kraeuter, 2007; Schulte, Lipcius and Burke, 2018; Morson *et al.*, 2018). Using values of 5% vs 20% can results in millions more oysters being assessed as being available for catch that are not there. Likewise use of a value of 20% vs 10% will underestimate the population size of oysters by 50% creating conflict between fishers and statutory authorities. To address this and provide evidence of what dredge efficiency assumptions would be reasonable, a series of experiments were designed to assess the catch efficiency of a standard native flat oyster ladder dredge using patches of known oyster density and distribution. Specifically, we addressed what the average and range of dredge efficiencies are across different mixed-sediment ground types (e.g. hard shell vs mud dominated), oyster densities (e.g. 1 vs 2.2 m^{-2}) and oyster distributions (uniform vs clumped). In addition we examined whether second passes of the dredge had different efficiencies to first passes and whether season, known to influence seaweed biomass caught in the dredge, had an effect on dredge efficiency.

2 Methods

2.1 Site selection

A site for this study required safe access to the lowest intertidal areas of a representative estuarine system. The lowest intertidal that is revealed on only a few tides per year represents as close to the subtidal habitat that flat oysters are found in Essex estuaries. Additionally due to the protected nature of most coastal and marine sites, another requirement was legal access – we required access to a site already granted permission for oyster dredging or similar activities – e.g. a private fishery. Lastly we sought a site to work where ideally native oysters were not currently present or uncommon so that density of oysters could be fully controlled. The lowest intertidal areas of Thirslet creek on the Blackwater estuary near Tollesbury, Essex was selected as having both these properties (between 51°44′9.97″N, 0°48′57.46″E and 51°44′9.61″N, 0°49′13.06″E; see west/north-west creek in Fig. 1 in Cameron *et al.*, 2023). In addition the ground at this point was relatively hard underfoot due to the presence of shell and gravel on the site that made working conditions safer and more representative of local subtidal oyster habitats of mixed sediment (Allison *et al.*, 2020).

Six and four experimental oyster dredge beds were created using tall marker poles that would be seen when dredging occurs when the tide is high, in April and September respectively. Each bed was 50 m long by 2 m wide to accommodate the 1.2 m wide ladder dredge. In April, the beds ranged from very hard, to mixed hard and soft ground, to a fully soft bed at the easterly end of the site that was covered in a 10–20 cm layer of very soft mud above the harder ground. There were two replicates of each bed type in April 2021. In September only four beds were possible and there were two each of the hard beds and the mixed hard/soft beds. Across all beds there were shallow drainage creeks that were always softer that the surrounding habitat. The beds therefore represented a range of habitats that could be found in the lowest intertidal stretching into the subtidal (Fig. 1). The field research was undertaken in April and September 2021 to

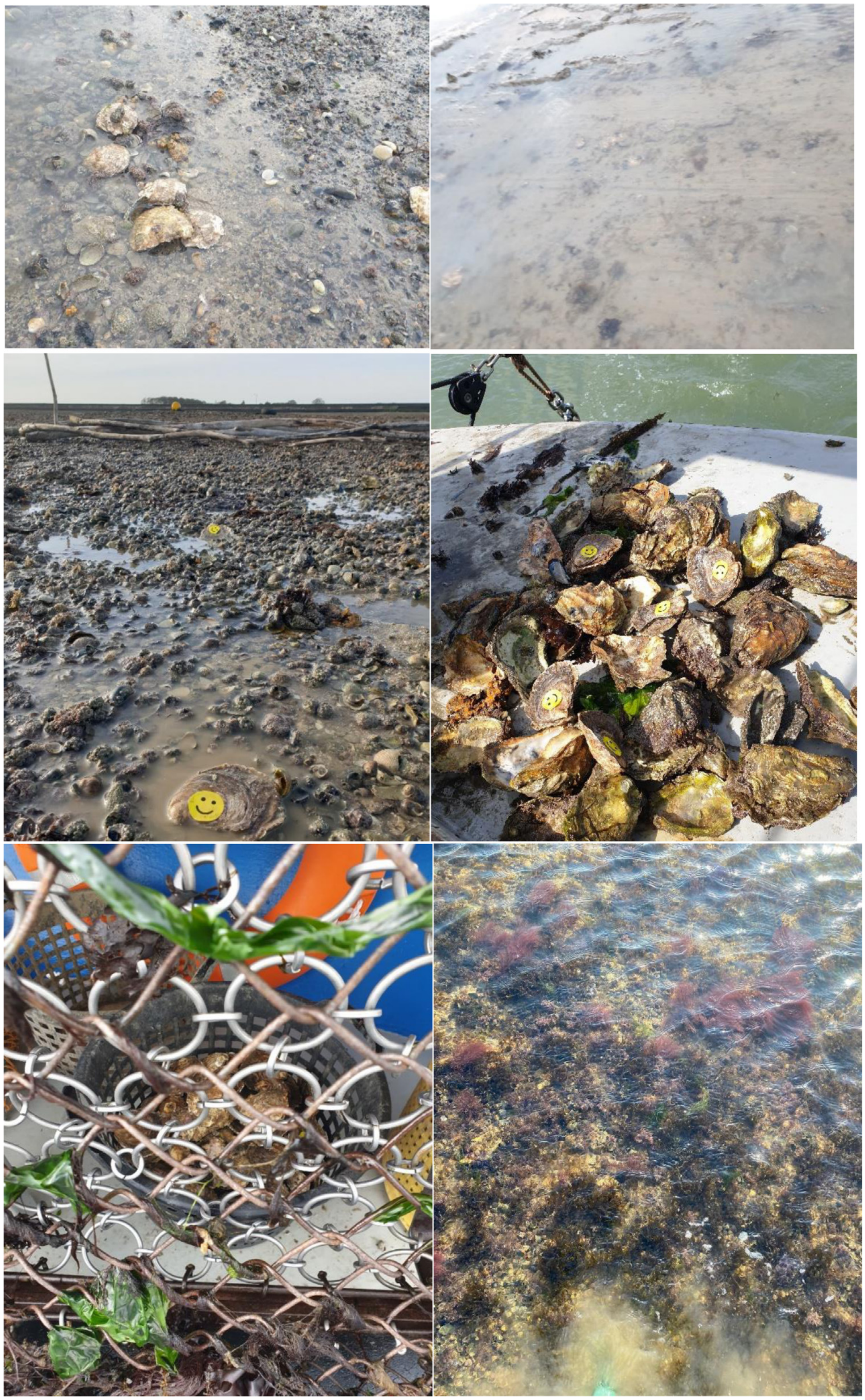

Fig. 1. Clumped flat oysters post dredge at the next low tide on hard ground (top left) and on softer ground where the dredge marks in the soft sediment can be seen and the oysters are pressed into the sediment. Flat oysters in a uniform 1 m^2 density treatment in April over hard ground showing low weed biomass (middle left). Oysters were marked with a yellow sticker at the outset, but due to negligible flat oysters being present at Thirslet creek this was not needed and was stopped. Partially sorted landings on the sorting table after an experimental dredge showing catches of dead shell, rock oyster and flat oyster (middle right). The ladder dredge was fixed with a ring escape mesh of 45 mm diameter (bottom left) and a comparison of the same experimental dredge bed as can be seen in the top and middle-left in April but in September with increased weed biomass (bottom right).

represent low and high seaweed biomass periods respectively as advised by local oystermen (also see Lown, 2019).

2.2 Deployment of oysters

Flat oysters were bought from Tollesbury and Mersea Oyster Company and were landed within a week of experimental deployment. All oysters used in the study represented animals of at least minimum legal landable size of 70 mm (height – as measured from umbo to outer edge). Therefore the efficiency of the dredge was being measured in its ability to catch adult oysters that the dredges are designed to catch.

Oysters were taken to Thirslet creek and were deployed on the experimental beds at known densities in either uniform or clumped distributions on foot. For 1 oyster m^{-2}, uniform distributions were deployed by placing an oyster at the diagonal of each 1 m (length) by 2 m (wide) square metres such that they alternated as being closer or more further part. At higher or lower densities this was adjusted by deploying at shorter or longer intervals along the bed.

There are 40 dredge data points in April 2021, and 16 in September 2021, thus restricting us to only four experimental beds in September compared to the six in April. For clumped distributions, oysters were deployed in a clump of ten oysters every 10 metres along the bed. In April 2021, for uniform and clumped distribution realised trials densities of 1 and 2.2 oyster m^{-2} were used. In September 2021, 1 and 1.2 oysters m^{-2} were used and only with a uniform distribution.

Care was taken to present oysters to the dredge in a range of orientations. This included facing lid up vs down and umbo facing various directions relative to the dredge. In addition, oysters were either very lightly pressed, more firmly pressed or deliberately stuck upright into the sediment to reduce movement caused by the tides and to provide reasonable range of presentations that might be experienced by those undertaking surveys or fishing.

Between each dredging session within April and September, the number of oysters caught by the dredge were recorded and therefore could be returned to the experimental beds at the next low tide for re-setting of the experiment. After the April session, oysters were left on the site but live animals gathered up prior to and used within the September session.

The background density of *Crassostrea gigas* across the site was estimated using 1 m^2 quadrats. While not a primary objective, it would provide information on the efficiency of the same dredge in catching this species. On average, the size of *C. gigas* oysters at this site was very large, most often beyond marketable size.

2.3 Dredging

Experimental dredging was undertaken using an oyster dredging boat used by the Tollesbury and Mersea oyster company – "Native". Native is a 10 m dredger with 95 hp engine hosting a twin barrel hydraulic winch. Attached to the winch was a 1.2 m (four foot) standard ladder dredge with 22 mm ladder rung spacing's and 45 mm diameter mesh ring size. This is similar but not identical to the survey ladder dredge used by KEIFCA in their research surveys of the BCRC MCZ.

Dredging was undertaken by lining up the vessel with the marker poles and keeping the port side of the vessel in a straight line approximately 1 m from the poles. The ladder dredge was deployed off the starboard stern of the vessel as the starting marker of each bed was approached. Dredge tows were undertaken at 1.8 – 2.2 knots across all replicates. Dredges were lifted as the end bed marker was passed, the skipper emptied the dredge onto the sorting table, and the number of live native oysters and *C. gigas* were counted by the researcher and checked by a witness and this was usually the skipper. If live oysters were retained on the ladder face and had not yet passed up into the bag, and they could be retained by hand by the skipper this was permitted as that is what would happen when fishing. If they fell back into the sea before they could be retained they were not counted. Capture of native oysters that were already present on the site occurred but was very rare (3 oysters). It was easy to differentiate between oysters already on site and those we brought onto the site as Thirslet flat oysters were dark brown to dark green coloured whereas the oysters supplied for the subtidal several order were pale brown, beige and metallic purple. Oysters thought to be already on the site were discounted from the analysis.

2.4 Experimental design and analysis

To maximise the replication available to test specific hypotheses we first tested and found there was no difference in dredge efficiency between first and second passes of the dredge across all attempts (paired *t*-test, see results). As only two ground hardness types were available in September compared to three in April, oyster distribution and ground hardness interaction effects on dredge efficiency were examined with only April data. Likewise, due to the lack of the softest ground type in September, data from the soft ground was excluded when looking for differences in dredge efficiency between seasons. Few passes resulted in zero capture and any that did were only included where it was felt they were a real zero – that the dredge had passed over the bed. This occurred on three occasions and all three events are included in the following analysis. Efficiency data were analysed as the percentage of oysters caught relative to those that were catchable. Efficiency data were not normally distributed but results from linear models with normal Gaussian error and general linear models with either binomial or quasibinomial error were qualitatively similar. The results from the linear model, assuming normality, are presented in the main text.

3 Results

There was no statistically significant difference in dredge efficiency between the first and second dredge pass across all plots and seasons (paired test $t_{1,28} = 0.58$, $P > 0.5$; Fig. 2). Dredge pass was therefore no longer included as an explanatory variable and the data sets combined. There was also no significant difference in the dredge efficiency between the April and September seasons using all data ($F_{1,56} = 0.45$, $P > 0.5$; April mean = 10.0% median 7.63%; September mean = 11.37% median 10.94%; Fig. 2), and this result was not influenced by excluding the results from dredging on the softest ground types only present in the April fieldwork period.

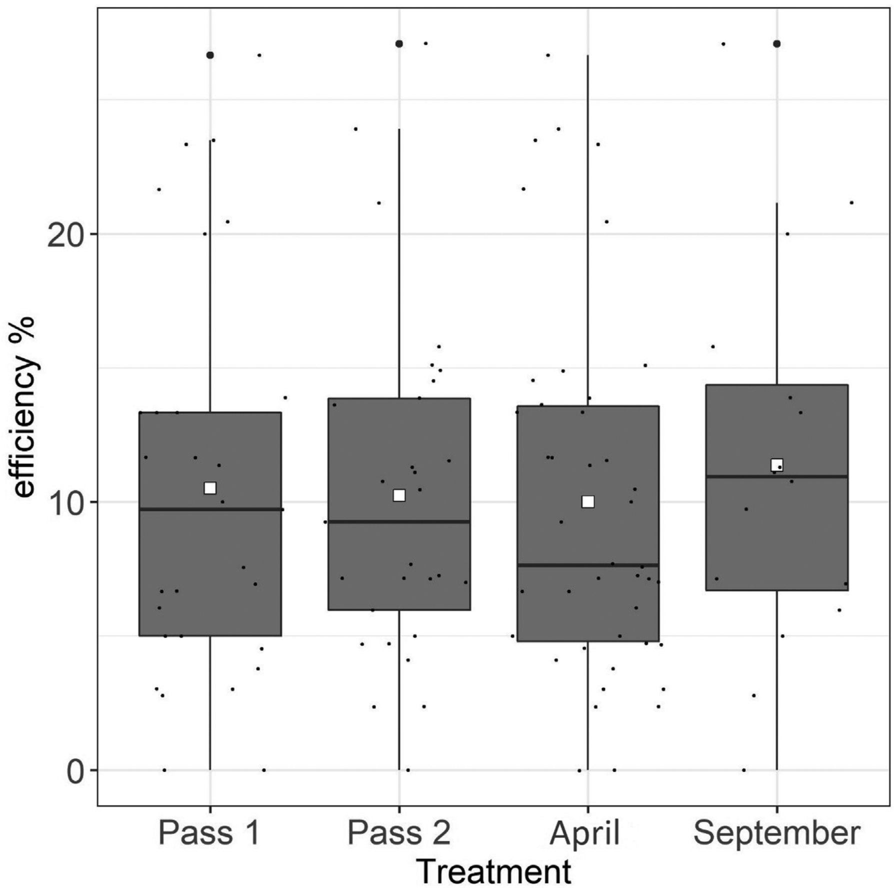

Fig. 2. Median (solid line), mean (white square), inner quartile and range (box and whiskers) and any outliers to the range (bold filled circles) showing all raw data (smaller points) for flat oyster dredge efficiency by 1 st and 2 nd dredge pass (April and September combined) and season (Pass 1 and 2 combined). While there is a trend towards higher efficiency values in September when seaweed and algae biomass was higher (see Fig. 1), there was no statistically significant difference in efficiency between seasons.

As only two of the three ground types and uniform distributions were examined in the September fieldwork period, the effects of ground type and oyster distribution were examined separately for each fieldwork period (Figs. 3 and 4). The distribution of oysters on the seabed, uniform vs. clumped and the hardness of the ground over which the dredge is operated has a statistically significant and interactive effect on the dredge efficiency (Distribution Ground hardness $F_{2,36} = 4.51$, $P < 0.02$; Fig. 3). While average efficiency is higher when oyster distributions were uniform, efficiency increases with increasing ground softness with uniformly distributed oysters (e.g. hard ground to soft $+10.63 \pm 3.9$ (2SE)% efficiency), but this does not happen when oyster distributions are clumped (e.g. hard to soft ground -2.64 ± 2.9 (2SE); Fig. 3). In September where there was less replication there was no significant effect of ground type detected with uniformly distributed oysters between hard and mid-hard ground – the two hardest ground types ($F_{1,14} = 2.7$, $P > 0.1$; Fig. 4).

There was no significant interaction between oyster bed density, distribution and ground hardness on dredge efficiency in the more complete April fieldwork data. But density did influence efficiency, for example an estimated 4.2% decline in dredge efficiency when oyster density increased from 1 to 2.2 oysters m^{-2} ($F_{1,35} = 9.45$, $P < 0.01$; Fig. 5). When including the September data and examining whether there was an oyster density and distribution interactive effect on dredge efficiency we found no effect of the interaction between density and distribution (density distribution – $F_{1,54} = 0.005$, $P > 0.98$), but again a significant effect of oyster density on dredge efficiency (density $F_{1,55} = 4.07$, $P < 0.05$; Fig. 6).

The average naturally recruited rock oyster (*Crassostrea gigas*) density across the site was 2.57 m^2 (range 0–11 m^2) of predominately large oysters, i.e. greater than 100 mm shell height (umbo to outer edge). The average 1 st pass efficiency of the dredge for this species was 10.23% (range 2.56–22.43). But there was a noticeable decline in the efficiency over time where efficiency declined from a two day average of 14% to 6% between the beginning and end of the dredging periods on the experimental beds. This is most likely due to the oysters being removed from those beds and not being replaced, and so the 14% dredge efficiency value is likely more robust.

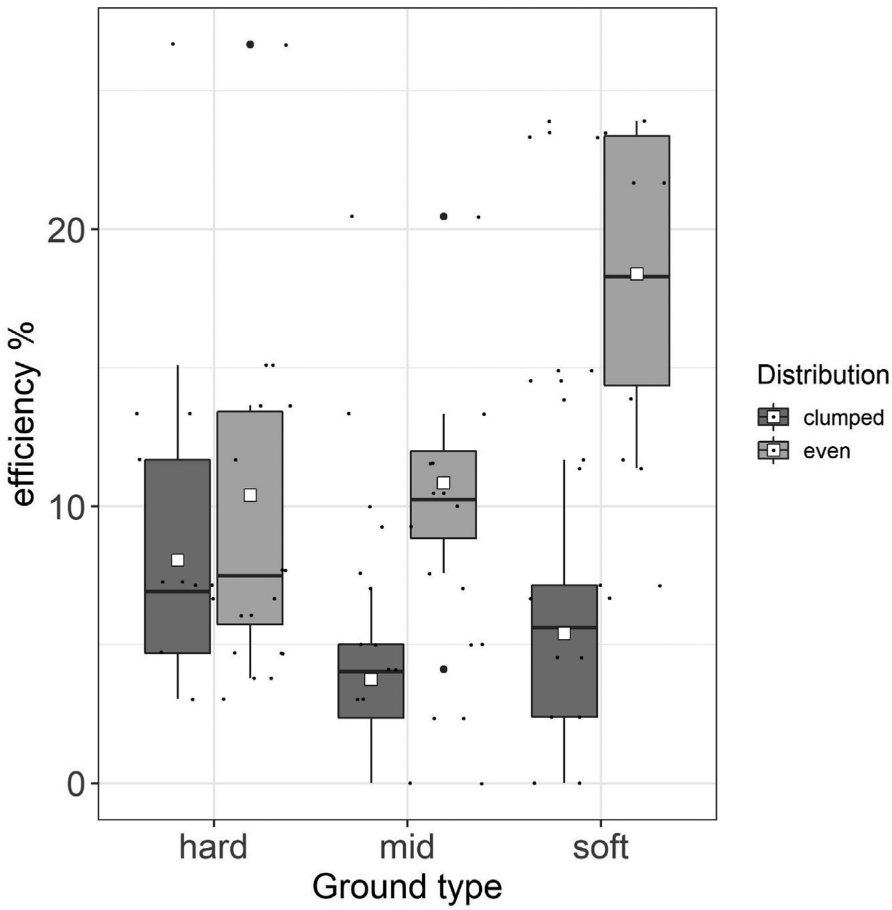

Fig. 3. Median (solid line), mean (white square), inner quartile and range (box and whiskers) and any outliers to the range (bold filled circles) showing all raw data for flat oyster dredge efficiency by ground type (hard sediments, mid =mix of hard and soft areas, soft sediments) and oyster distribution (evenly or uniformly distributed vs clumped). Data from April only. Dredge efficiency declines with increasing ground softness when oyster distributions are clumped, but increases when evenly/uniformly distributed.

4 Discussion

We experimentally measured the catch efficiency of ladder dredges used for harvest and surveys across the UK and Europe for *Ostrea edulis* and found the median efficiency to be 10.7%. The average efficiency of this oyster ladder dredge on larger rock oysters, *Crassostrea gigas*, was similar but it must be noted that this species was not experimentally replenished, therefore the initial few days average of 14% may be more appropriate.

The most striking result was how flat oyster dredge efficiency responses to ground type differed dependent on the distribution of oysters on the experimental beds – uniform vs clumped. Oyster dredge efficiency increased over softer ground when oysters were uniformly distributed, but when oysters were clumped together the efficiency declined as ground became softer. Post dredge observations of the dredge tracks at low tide suggested that the dredge hitting a large hard clump while gliding through the soft sediment may cause the dredge to bump over the oysters via reactionary force, or otherwise push the whole clump down into the sediment (Fig. 1). This does not happen over harder ground as post dredge observations confirmed that when the dredge hits a clump it scatters them forward rather than down, picking some of them up. This could be due to surface tensions between the oysters and the substrate they are embedded in – which would be high in soft estuarine muds but lower in harder sandy or gravel substrates.

Understanding native oyster spatial distributions and densities and understanding how these interact with the wider environment, disease risks, Allee effects and ecosystem function remains poorly understood (zu Ermgassen *et al.*, 2020). Yet this is an important set of questions as it could mean adopting a 6% vs. 18% dredge efficiency assumption over soft ground for clumped versus uniform oyster distributions respectively. Little is known about oyster distributions although it is expected that they will be more clumped than uniform. Over what scale this distribution is measured will also make a difference. In the BCRC MCZ in Essex, from surveys conducted in 2018 by 100 m dredge tow in previously oyster positive areas (Lown *et al.*, 2020; Lown *et al.*, 2021), a variance to mean ratio of the catch per dredge across all sites was 5.47. Excluding a very high ratio at the mouth of the river crouch caused by a single very high density mixed patch of

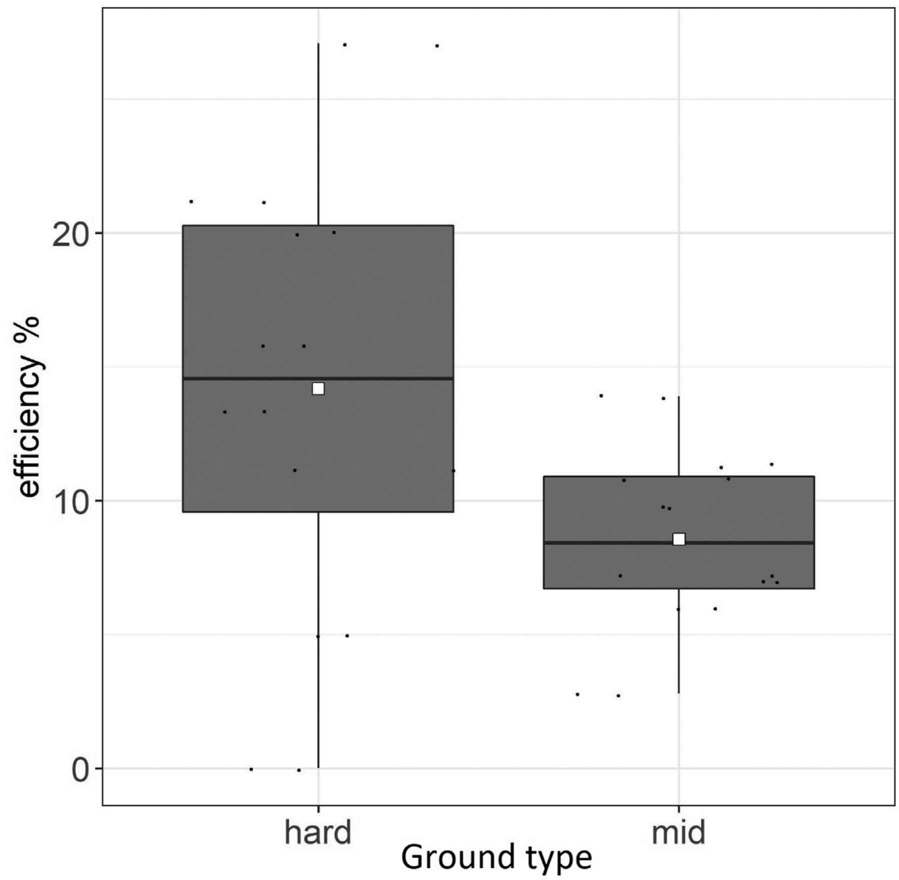

Fig. 4. Median (solid line), mean (white square), inner quartile and range (box and whiskers) and any outliers to the range (bold filled circles) showing all raw data for flat oyster dredge efficiency by ground type (hard sediments, mid = mix of hard and soft areas) for uniformly or even distributed oysters in the September session only. Despite appearance of trend towards reduced efficiency moving from hard to mixed ground – this is not a significant difference and matches the result from April (Fig. 3).

non-native rock oyster and native flat oyster the mean ratio is 3.12 (range 0.98–799). At the half kilometre scale that these dredges were undertaken (one at centre of 1 km^2 and 1 at corners of same square – with most continuous patches at 2 km^2 in size – n = appx 10 per ratio estimate), we can say the oysters are likely to be more clumped in distribution. Few estimates are available at a smaller scale but 0.125 m^2 grab samples taken in a high density mariculture site in the River Blackwater in 2012 resulted in a ratio of 5.09 (mean density 6.6 m^2). This also points to a patchy and clumped distribution at a much smaller scale, noting that in mariculture sites natural clumps of oysters are likely to be broken up and redistributed by growers to aid product development. If it is the case that non-uniform distributions and soft ground are characteristics of the ground being surveyed by dredge – then a median value of 10% efficiency may be too high and values of 5% may be more appropriate.

The most important but perhaps not unexpected result was how dredge efficiency declined with increasing oyster density (e.g. 4.2% decline between 1 and 2.2. oyster/m^2). Density dependent shellfish dredge efficiency has been observed before with *Crassostrea virginica* (Morson *et al.*, 2018). While working across a broader range of much higher densities, Morson *et al.* (2018) also observed catch efficiency to decline with increasing oyster density in *C. virginica*. The danger of this is that Catch per Unit Effort that is often used to describe shellfish abundance assumes that the relationship between fishing effort and catch is constant, density dependent dredge efficiency violates this assumption. For this reason where density dependence in catch is observed, CPUE is discouraged due to the likelihood of hyperstability as catch declines or when surveying areas of low shellfish density (Morson *et al.*, 2018). CPUE is currently used in a range of UK native flat oyster fisheries and recovery areas and many of these experience very low density; we would advise practitioners to stop using CPUE and determine an appropriate dredge efficiency for their area.

We have presented a study of experimental estimation of ladder dredge efficiency for the harvest and survey of native flat oysters and our results suggest a median dredge efficiency value of 10%, with a range of 5 to 25% for confidence intervals. There are features of sites in the southern North Sea where this work was undertaken, lower oyster density and mixed sediments that suggest 10% should be adopted as a

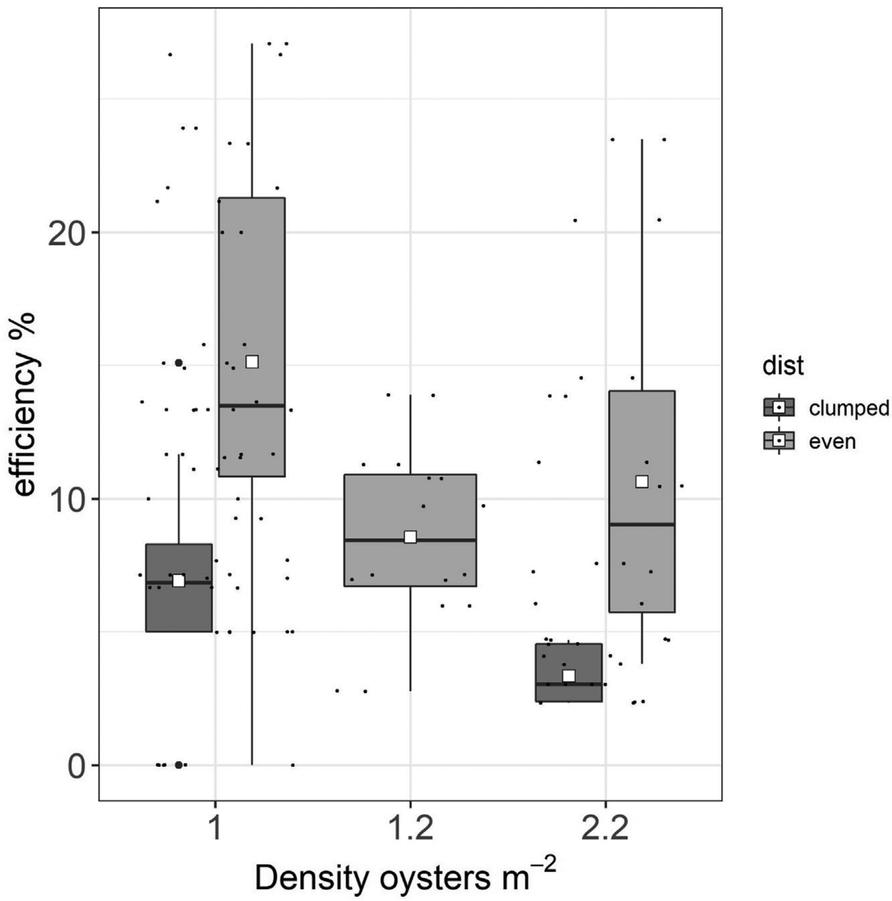

Fig. 5. Median (solid line), mean (white square), inner quartile and range (box and whiskers) and any outliers to the range (bold filled circles) showing all raw data for flat oyster dredge efficiency by oyster density and distribution on the bed for April and September data combined. Density of 1.2 oysters m^2 only occurred in September. Significant declines in dredge efficiency occur as density increases and is similar between the two different distribution types. While more density treatments would be valuable this suggests that Catch efficiency changes with density. If this relationship is robust to further work it would suggest that efficiency values are high when oyster densities are low – e.g. 20% as density approaches 0.5 m^2.

suitable national figure. However the distribution of native oysters being more clumped than uniform may mean even this dredge efficiency value is too high and a value of 5–8% may be more appropriate. Justifications for using any efficiency figures must be based on ground types, known oyster distributions or density – where low oyster densities would be characterised by a likelihood of higher efficiency – e.g. 10–20% – not lower efficiency assumptions to artificially increase abundance estimates.

The motivation for this work was the management of the Blackwater, Crouch, Roach and Colne Marine Conservation Zone designated in 2013 to protect and restore native European flat oysters, *Ostrea edulis* and their habitats or "beds". At 284 km^2 in size with low water visibility and high sediment loads this site has always been monitored by ladder dredge survey over alternative methods such as grabs or video surveys. An accurate estimation of dredge efficiency was therefore important for setting baselines and trends of oyster abundance against which protection and recovery could be judged. This can be achieved by taking grab and dredge samples in the same locations and such an approach in the River Blackwater in Essex led to efficiency values of 14% (range 4.6–42%; corrected for 1.2 m dredge, Allison, 2018). However two further attempts in the same study returned no oysters by multiple grab samples where dredges did find them, so this method is not guaranteed and excludes that grabs may have their own efficiency values below 100% (Schulte, Lipcius and Burke, 2018). As introduced above, a literature review conducted by English statutory authorities in 2016 and subsequently developed by Lown (2019) determined an average dredge efficiency value of 20% was appropriate – with a range of 10–30% being appropriate for estimating confidence intervals (Lown, 2019; Lown *et al.*, 2020; Lown *et al.*, 2021). This 20% dredge efficiency value has been used in determining the baseline and trends in abundance of flat oysters in the BCRC MCZ since 2015, and to predict how this population will respond to harvesting (Lown *et al.*, 2020), to better understand oyster density thresholds of associated species complexes (Lown *et al.*, 2021), to conduct several local stock surveys and to provide a review of evidence for measuring oyster density and what densities are currently observed across the MCZ (Cameron 2021).

The conclusion of all of the above exercises are influenced by the adoption of a lower dredge efficiency value but in a predictable way – that the baseline starting conditions of the MCZ post designation and any stock abundance in a fisheries context is higher – potentially double or more – what was estimated previously. This change does not affect trends, but it would influence how many years a population might be expected to require to reach a given threshold or biomass trigger for harvest. More importantly it would influence the estimated range and frequency of densities of flat oysters observed in the MCZ where we had previously found that the vast majority of dredge sampled sites in the MCZ were below 1 oyster m^2 and 95% less than 2.5 m^2 (Lown *et al.*, 2020; Lown *et al.*, 2021) – this would become 2 oysters m^2 and 5 m^2 respectively under a 10% dredge efficiency.

This is the first fully experimental approach to ladder dredge efficiency for native oysters and has observed the importance of several features of native oyster habitat, distribution and abundance that can influence fieldwork assumptions. We would recommend that a research team experimentally estimates the efficiency of their flat oyster sampling methods for their local area, or otherwise use median and range of estimates we have discovered in this study.

Acknowledgements

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Data availability statement

The data have been published and are available here https://repository.essex.ac.uk/.

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Supplementary Material

Figure S1. Frequency distribution of oyster ladder dredge catch efficiency data expressed as a percentage from experimental assessments carried out in April 2021. The data are not normally distributed but were normalised by an appropriate transformation -e.g. Square root of the arcsine of the catch efficiency expressed as a fraction (Fig. S2).

Figure S2. Frequency distribution of oyster ladder dredge catch efficiency data expressed as a the arcsine square-root transformation of a fraction of total oysters available to catch from experimental assessments carried out in April 2021. This distribution passes a Shapiro Wilks normality test ($W = 0.9684$, $P = 0.2916$).

Table S1. General linear model results of dredge efficiency data expressed either as percentage or fraction of maximum potential oyster catch with different data transformations, error assumptions or overdispersion corrections. All models obtained the same minimum adequate model where there was an interaction between ground type and oyster distribution, but only a main effect of oyster density. There are no qualitative differences between the conclusions reached from the four models when interpreting the results presented in Figure 3 in the main manuscript.

The Supplementary Material is available at https://www.alr.org/10.1051/alr/2023021/olm.

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