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Missing the full story: First estimates of carbon deposition rates for the European flat oyster, *Ostrea edulis*

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Title: Missing the full story: First estimates of carbon deposition rates for the European flat oyster, *Ostrea edulis*

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Abstract

1. Globally, momentum to restore damaged habitats has been increasing. For example, the number of European shellfish restoration projects has quadrupled in the past three years. In line with the increasing focus on both restoration and climate change mitigation efforts, the present study highlights how these two practices can complement each other.
2. By developing a full understanding of the ecosystem services (functioning, supporting, regulating and cultural) provided by a habitat, it becomes possible to quantify overall ecosystem function. This evidence is key in advising policy makers, restoration funders and marine spatial planners on the connection between keystone species restoration, ecosystem service restoration and conservation management.
3. The present experimental study quantifies the active and passive sediment deposition associated with the European flat oyster (*Ostrea edulis*) and the organic and inorganic carbon fractions of the deposits. Treatments included 'dead', 'live' and control to account for i) passive deposition, ii) biodeposition and passive deposition and iii) background deposition respectively. By utilizing these data, the expected carbon deposition associated with a restored flat oyster bed was investigated.
4. The experiment was conducted *ex situ*, with natural sea water input. Covariate data on temperature, suspended particulate influx, salinity and oxygen availability were recorded. Enhanced sedimentation (2.9 times) and organic carbon deposition (3 times) were observed in the presence of living oysters, compared to the control. The shell structure of the oysters had no influence on passive sedimentation in the present study.
5. The enhancement of benthopelagic coupling by the European flat oyster, evidenced here for the first time, is contextualized from the perspective of quantification of ecosystem service provision for both restoration practices and blue carbon store management. The data produced in this study are discussed comparatively with work which has focused on other species from both Europe and the USA.

Key words

climate change, coastal, ecosystem services, estuary, feeding, invertebrates, reef, restoration

1. Introduction

There is increasing recognition that marine habitats have been lost, that baseline habitat health and extent are not what they were, and that there is scope for ecological restoration (Alagona, Sandlos, & Wiersma, 2012; Duarte et al., 2020; Pauly, 1995; Pogoda et al., 2019; Sáenz-Arroyo et al., 2005). Human populations rely on the world's ocean for goods and services, but population growth and a changing climate have adversely affected the functioning of marine ecosystems (Duarte et al., 2020; Halpern et al., 2012; Hoegh-Guldberg & Bruno, 2010). As a consequence, the number of restoration projects has escalated rapidly across a range of marine and terrestrial ecosystems, and they are increasingly predicated on the improvement of Ecosystem Services (ESS) (Bayraktarov et al., 2016; Beck et al., 2011; Haddad et al., 2015; Orth et al., 2006; Pogoda et al., 2019; zu Ermgassen et al., 2020).

Ecosystem services of degraded habitats are often unquantified, therefore expected outcomes from restoration tend to be modelled from comparable habitats elsewhere (*cf* Kellogg et al., 2014; Newell, 1988; zu Ermgassen et al., 2020). This undermines the valuation of restoration work by creating uncertainty in the estimate of ESS and doubt over claims of positive environmental and socio-economic outcomes (Barbier et al., 2011; Beck et al., 2011; Coen et al., 2007; Herr et al., 2017; van der Schatte Olivier et al., 2018; zu Ermgassen et al., 2020). A lack of direct evidence and understanding of ESS also impedes the formation of policy and best practice regarding the protection and enhancement of marine habitats and the promotion of 'climate resilience' (Bates et al., 2019; Herr et al., 2017; Siikamäki et al., 2013; SNH, 2019). In order to integrate carbon sequestration of a specified marine feature into marine management decisions, evidence must first be provided on rates of carbon accretion and loss, as well as feature sensitivity to disturbance and environmental changes (Herr et al., 2017; Ullman, Bilbao-Bastida, & Grimsditch, 2013).

Bivalve habitats, especially oyster beds, are considered some of the most imperilled habitats on earth (Beck et al., 2011). Drivers of loss include over-fishing, disease and shell collecting, as well as the impacts of a changing climate, e.g. increased competition with non-native species and ocean acidification (Diederich et al, 2005; Kowalewski, Domènech, & Martinell, 2014; Laing, Walker, & Areal, 2006; Mazik et al., 2015; Waldbusser et al., 2014). Their diminished status has resulted in a recent escalation in the number of projects to restore degraded bivalve populations, including the Billion Oyster project in the USA (Burmester & McCann, 2019), the Shellfish Reef Restoration Network in Australia (Gillies, Creighton, & McLeod, 2015), the NORA consortium in Europe (Pogoda et al., 2019) and the Dornoch Environmental Enhancement Project (DEEP) in Scotland (Fariñas-Franco et al., 2018). For the European flat oyster (*Ostrea edulis*), however, quantification of ESS remains poorly understood and as such is a research priority with regards to habitat restoration and integration of ESS into marine policy (van Der Schatte Olivier et al., 2018; zu Ermgassen et al., 2020).

The European flat oyster was once abundant across Europe; the species' natural distribution ranges from the Norwegian Sea through to the Atlantic coast of Morocco (Laing et al., 2006; Pogoda, 2019), from the shallows to 50m in depth (Olsen, 1883; Thurstan et al., 2013). Depleted low-density populations (0.2-3.5 oysters m^{-2}; Cooke, 2003; University Marine Biological Station Millport, 2007) are documented throughout northern Europe (Laing et al., 2006), however, the recruitment to these populations and therefore health is considered to be hampered as a result of their low-densities (Pogoda, 2019). Higher population densities (≥ 5 oysters m^{-2}), around Sweden and the Danish Limfjord, have been linked to the restriction of habitat damage associated with dredge fishing (Pogoda, 2019; Thorngren et al., 2019).

High density populations of bivalve shellfish have the potential to create complex structures (*cf* Blomberg et al., 2017; Coolen et al., 2020; Fodrie et al., 2017; Thorngren et al., 2019) that provide refuge for fish and marine invertebrates, supporting biodiversity and fisheries (Coen et al., 2007; Kent et al., 2017*a*; Peterson, Grabowski, & Powers, 2003) and enhance bentho-pelagic coupling through water filtration (e.g. Kellogg et al., 2014; Kent et al., 2017b; Newell, 1988).The increase in structural complexity of the seabed caused by oyster beds, combined with the depositional activities of the living oysters, might be expected to result in the accumulation of not only carbonate shell deposits but also sediment over time (*cf* Fodrie et al., 2017; Lindenbaum et al., 2008). Carbonate accumulation by bivalve beds is addressed by Burrows et al. (2014; 2017), although no values for sediment carbon are presented. Whether carbonate accumulation represents a source or store of carbon remains unclear (Fodrie et al., 2017; Ware, Smith, & Reaka-Kudla, 1992) because CO_2 is released during the process of calcification, but carbon is stored as a part of the shell growth of the organism (Fodrie et al., 2017; Frankignoulle, Canon, & Gattuso, 1994; Ware et al., 1992). European flat oysters are suspension feeders, actively removing suspended particulate from the water column, producing faeces and pseudofaeces. Bivalves have therefore been used as bottom-up mitigation of eutrophication in the USA, where the American oyster, *Crassostrea virginica*, regulates regeneration of nitrogen and phosphorus (Kellogg et al., 2013; 2014; Newell et al., 2006). The filtration capacity of oysters in Chesapeake Bay was estimated to have declined by 85% prior to restoration (zu Ermgassen et al., 2012) and restoration has therefore been justified on the basis of the expected recovery of regulating services (Kellogg et al., 2014; Newell, 1988).

In the past decade, work aiming to quantify carbon budgets in various ecosystems has increased sharply, with a bias towards vegetated habitats in coastal ecosystems e.g. saltmarshes, seagrasses and mangroves. Recently, the potential carbon storage capacity of deep-sea habitats, sea lochs and calcifying biogenic reef formers has been recognized. Acknowledgement of the role of these habitats in the carbon cycle has highlighted that there remain extensive knowledge gaps in both accretion and erosion rates, carbon budgets and store extents as well as the role of buried carbonate material (Burrows et al., 2014; 2017; Fodrie et al., 2017; Herr et al., 2017; Ullman et al., 2013). The regulatory services provided by the European flat oyster are one of these gaps (van der Schatte Olivier et al., 2018; zu Ermgassen et al., 2020).

In the present study, the rate of biodeposition of the European flat oyster was examined in an aquarium system fed continuously with natural sea water. The assumed active (resulting from feeding, referred to herein as biodeposition) and passive (as a result of the physical structure of the shells) components of sedimentation were quantified and the chemical properties of the deposits examined, including carbon content. The following hypotheses were tested: 1) the rate of particulate deposition will be enhanced by the presence of live European flat oysters; 2) the deposition of carbon will be enhanced by the presence of live European flat oysters; 3) European flat oysters physical structure will increase sedimentation through passive deposition.

2. Methods

Quantifying active and passive sedimentation

Quantification of passive and active depositional rates associated with the European flat oyster was undertaken at the St Abbs Marine Station, Scottish East Coast, between 16th April and 26th April 2019 (10 days). Localized food depletion was reduced by the continuous flow-through of sea water, delivering food particles. A reduction in food may have otherwise created variation in feeding response (Cranford, Ward, & Shumway, 2011). Five 450L fibreglass tanks were fitted with baffles (Figure 1) to promote a uniform flow. Maximum flow in the aquarium system was matched at 0.08 cm s^{-1} across the five tanks and volumetric flow rate was monitored throughout the experimental period. Water samples (3 x 4L) were taken daily and vacuum filtered on ashless Whatman filter paper (2 µm pore size; Navarro and Thompson, 1997), to estimate the suspended particulate food material available. Filters were dried for 48 hours at 60 °C, left to cool and weighed to determine total particulate mass. Temperature (°C), salinity (ppt) and dissolved oxygen (mg L^{-1}) were also recorded (Pro DSS logger, YSI Incorporated, Ohio, USA).

Experimental units were 3.5 litres with a 2cm thick basal concrete layer for ballast. Scouring pad material was used to help retain deposited sediments (adapted from Kent et al., 2017b). Within each of the five fibreglass tank three experimental units (one of each treatment plus a control) were deployed in a random order to avoid any positional biases (Figure 1). Control units were controls for background deposition. In ‘dead’ and ‘live’ treatments, three oysters (scaling to a density of 75 oysters m^{-2}; Hugh-Jones, 2003; Tully & Clarke, 2012) were deployed in the same configuration (Figure 1). Oyster size was standardized across units (Height = 7.4cm, ±0.38SD, Width = 6.3cm, ±0.22SD, Depth = 1.6cm, ±0.25SD, wet weight = 56.3g, ±5.5SD). ‘Dead’ treatments had empty oyster shells with their valves bound together with concrete; representing the physical structure of an oyster bed and therefore the passive influence on deposition caused by a disruption of flow. ‘Live’ treatments had live oysters and represented both the active component of deposition caused by feeding activities (biodeposition) and passive deposition as outlined above. Each tank was covered with a shade net to eliminate disturbance from passing researchers and reduce natural light intensity. The clear roof of the marine station provided a natural light regime of approximately 15hrs 30mins of daylight per day.

Water-tight lids were placed on all units for recovery. Units, scouring pads and oysters were rinsed into a 5L bucket. The seawater-particulate suspension was then filtered, dried and weighed as previously outlined. Total particulate matter (TPM) deposition was calculated by subtracting the dry weight of the filter paper from the final dry weight. TPM deposition was scaled to g m^{-2} day^{-1} by dividing the weight of deposited sediment, by the area of collection, by duration of the experiment (Kent et al., 2017b). Active deposition per animal per day (mg $oyster^{-1}$ day^{-1}) was also calculated by subtracting the deposition rate measured in the ‘dead’ treatment from that measured in the ‘live’ treatment and dividing by the number of days of the experiment and the number of oysters (3). Dried particulate matter was removed from the filter papers and then homogenized prior to further analysis.

Loss on ignition

Homogenized sediment subsamples (200mg) were ashed at 500 °C for 7 hours to determine total organic matter (TOM) (*cf* Howard et al, 2014). Samples were cooled, weighed, then ashed again at 950 °C for a further 15 hours to determine carbonate matter which will from herein be referred to as total inorganic matter (TIM) (*cf* Wang, Li, & Wang, 2011). Samples were then cooled and re-weighed and percentage TOM and TIM were calculated with the formulae below (Eq.1).

Eq.1 Percentage TOM or TIM= (weight lost/total particulate mass) x 100

Elemental analysis

The percentage carbon in sediment samples was determined through CHN elemental analysis (*cf* Matejovic, 1993). Subsamples of approximately 1.7 milligrams of homogenized sediment were encapsulated in tin then analysed for %C (total carbon). Subsamples of homogenized sediment were acidified overnight with 0.1N HCl to remove carbonates, rinsed with DI water and dried for 48 hours at 60 °C (*cf* Howard et al., 2014). Acidified subsamples were then analysed for %C (organic carbon (OC)). The difference between total carbon and organic carbon was then determined to identify the inorganic carbonate carbon fraction (referred to as IOC). Sediment standard B2178 (Elemental Microanalysis Limited, Devon, UK) was used as a reference sample, to ensure machine calibration.

Statistical analysis

All statistical analyses were undertaken in IBM SPSS Statistics 22. Data were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Levene's test). Where assumptions of a parametric test were violated, data were square root transformed. A one-way ANOVA was used to investigate whether treatment influenced deposition rate, followed by a Tukey post-hoc test to determine differences between treatments. TOM, TIM, IOC and OC deposition rates were also calculated as a proportion of TPM to allow for comparison with work presented by Kent et al. (2017). Where data did not meet assumptions of a parametric test and were not suitable for transformation a Kruskal-Wallis test was selected instead.

3. Results

Environmental covariate data

Throughout the experiment the tank water temperature was measured at 8.3 °C (±0.7SD), salinity 34.3ppt (±0.1SD) and dissolved oxygen 9.46mg L^{-1} (±0.30SD), average suspended particulates in the sea water were 0.08g L^{-1} (±0.03SD).

Total deposition

Significant differences were observed between treatments (Table 1; Figure 2a; ANOVA, F= 28.02, $p < 0.001$) such that live oysters caused the deposition of 2.9 times more material per m^2 than both the control (TUKEY HSD, $p < 0.001$) and 'dead' treatments (TUKEY HSD, $p < 0.001$). There was passive deposition in both the control and 'dead' treatments but no significant difference between them ($p = 0.973$). Average active deposition was 34.9 mg $oyster^{-1}$ day^{-1}.

Loss on ignition

Data were normally distributed and variance homogeneous. TOM deposition was 2.9 times higher in the 'live' treatment (Table 1; Figure 2b; ANOVA, F= 31.73, $p < 0.001$) than in both the control (TUKEY HSD, $p < 0.001$) and 'dead' treatments (TUKEY HSD, $p < 0.001$). There was no difference in TOM deposition (Table 1, TUKEY HSD, $p = 0.97$) between the control and 'dead' treatments. When expressed as a proportion of TPM, TOM deposition differed between groups (Table 1; Figure 2c; Kruskal-Wallis ANOVA by ranks H = 7.25, p = 0.03). Pairwise comparison demonstrated a significant difference between 'dead' and 'live' TOM deposition by proportion (p = 0.009) but not between the control and 'live' treatment (p = 0.07). There were significant differences in deposition rate of TIM between groups (Table 1, Figure 2d; ANOVA, F = 5.88, p = 0.02), TIM deposition was significantly higher in the 'live' treatment when compared with the 'dead' (TUKEY HSD, p = 0.02). No differences were observed between the 'dead' and control (TUKEY HSD, p = 0.58) or 'live' and control pairwise comparison (TUKEY HSD, p = 0.09). When expressed as a proportion of TPM, differences in TIM deposition were non-significant between groups (Table 1; Kruskal-Wallis ANOVA by ranks, H = 3.87, p = 0.15).

Carbon deposition

Organic carbon deposition differed significantly between treatments (Table 1, Figure 2e; ANOVA, F= 30.37, p <0.001). Over 3 times more deposition was observed in the presence of live oysters than in the control (TUKEY HSD, p <0.001) and the 'dead' treatment (TUKEY HSD, p <0.001). No differences were observed between the control and 'dead' treatments (TUKEY HSD, p = 0.75). As a proportion of TPM, organic carbon deposition between groups was not significantly different (Table 1; Kruskal-Wallis ANOVA by ranks, H = 3.14 p = 0.21). There were no significant differences between groups with regards to inorganic carbon in the sediment deposition (Table 1; ANOVA, F= 3.33, p = 0.07), although inorganic carbon deposition on average was higher in the 'live' treatment.

4. Discussion

In the present study, benthopelagic coupling nearly tripled in the presence of live European flat oysters from an average TPM deposition of 0.91 g m^{-2} day^{-1} to 2.62 g m^{-2} day^{-1}. The average active deposition rate of an oyster per day was 34.9 mg, of which OC and IOC represented 1.6 mg and 0.9 mg respectively. The results demonstrate that the European flat oyster significantly contributes to the transport of particulate material and organic carbon from the water column to the seabed, but a passive depositional effect from the physical structure of the 'dead' oysters was not detected. The European flat oyster was shown, for the first time, to be a substantial contributor to benthopelagic coupling with significant implications for the understanding of carbon deposition rates and budgets within oyster beds.

Similar measurements of sedimentation have been made for other bivalve species, further demonstrating the importance of bivalves as facilitators of carbon deposition. Kent et al. (2017b) measured a doubling in sedimentation rates in the presence of live horse mussels (*Modiolus modiolus)* from 2.14 g m^{-2} day^{-1} to 4.29 g m^{-2} day^{-1}. Similarly, Giles, Pilditch and Bell (2006) demonstrated a 40% enhancement in sedimentation rates at a mussel farm (~410 g m^{-2} day^{-1}) compared with a reference site (~290 g m^{-2} day^{-1}). Unlike studies by Kent et al. (2017) and Widdows et al. (2002), the present study did not show passive deposition caused by the structure of the bivalve shells. The oysters were configured to represent a 'bed' structure lacking vertical relief or complexity (Brown et al., 1997). This appears to have resulted in negligible disruptive influence on flow, that otherwise might have caused the passive, turbulent deposition observed in other studies (Kent et al., 2017b; Styles, 2015; Widdows et al., 1998; 2002). High density populations of blue mussels (*Mytilus edulis*) create raised reef-like structures that increase sediment trapping and sediment stability when compared with adjacent habitat (Widdows et al., 1998, 2002). Sediment stability has also been shown to be non-linear in relation to density when communities were patchy (Widdows et al., 2002). Structural form is therefore likely to have a significant role in deposition rate (*cf* Fodrie et al., 2017; Styles, 2015). Increasing structural complexity with increasing relief directly influences seabed roughness, localized hydrodynamics and particle settlement velocities (Blomberg et al., 2017; Montserrat et al., 2009; Schwindt, Iribarne, & Isla, 2004; Styles, 2015; Widdows et al., 2002). Furthermore, in the present study the 'dead' treatment involved shell valves cemented together in a permanently closed position. Living oysters are not permanently closed, such that gaping may introduce fluctuations in the roughness of the oyster bed, altering localised hydrodynamics and the rate of particle settlement (Kitsikoudis, Kibler & Walters, 2019; Styles, 2015). Oysters however do not gape all the time, a percentage of gaping individuals across the bed at any one time will lead to small localized fluctuation in the benthic boundary layer across the bed that has not been accounted for in the present study. Overall, passive sediment deposition might be more evident in elevated oyster habitats as opposed to oyster habitats with low relief that were the focus of the present study.

Differences in both clearance and deposition rate are thought to be a product of spatial and temporal environmental variation (see Blomberg et al., 2017; Fodrie et al., 2017; Sanderson et al. 1996). Selection of food particles can be driven by changes in particulate size, shape, concentration, nutritional value and chemical composition (Arapov, Balic, & Peharda, 2010; Cranford et al., 2011; Shumway et al., 1985). Seasonality and environmental temperatures are also likely to moderate particle clearance rates, with lower temperatures reducing the production of faeces and psuedofaeces therefore suggesting lower carbon deposition rates would occur in winter and early spring (Haven & Morales – Alamo, 1966; Levinton & Doall, 2019; Tsuchiya, 1980). Furthermore, depositional rates can significantly vary as a function of weight; with either younger animals of the same weight as larger animals demonstrating higher clearance rates (Tsuchiya, 1980), or lower deposition per unit weight in larger oyster than smaller oysters (Ahn, 1993; Haven & Morales – Alamo, 1966). These factors as well as several others such as food concentration (Cranford, et al., 2011; Bayne, Hawkins & Navarro., 1987), turbidity (Grant, Enright & Griswold, 1990) and general carbon content of particles in suspension (Blomberg et al., 2017; Hedges & Keil, 1995; Montserrat et al., 2009) in turn would affect the deposition rate of both TPM and carbon. Overall, therefore, site and season can vary the composition of the food available and the rate at which corresponding sediment is deposited.

When expressed as a proportion of deposition, organic matter was proportionally higher in the presence of live European flat oysters, than in the 'dead' treatments (Figure 2c), however the proportional deposition of organic carbon did not follow the same trend (Table 1). In keeping with Kent et al. (2017) though, the proportion of TOM in TPM did not significantly differ between the control and 'live' treatment, it was also higher in the latter treatment. Total organic matter is more than just organic carbon (Howard et al., 2014), suspension feeders actively select and ingest food particles based on a number of factors as previously discussed (Arapov, Balic, & Peharda, 2010; Cranford et al., 2011; Shumway et al., 1985) this may therefore account for the increase in the proportional deposition of organic matter in the presence of live animals.

Emphasis on the role of marine habitats (e.g. mudflats, sea lochs, maerl etc.) in carbon sequestration, other than just those formed by primary producers, is increasing (Burrows et al., 2017; 2014; Herr et al., 2017). When considering calcifying organisms, however, studies tend to have focused on the inorganic carbon fraction in the form of calcium carbonate (see Burrows et al., 2014; 2017). Little attention has been given to sediment deposition as a result of the active and passive deposition associated with the organism and therefore a significant component of the carbon budget may have been overlooked (see Fodrie et al., 2017). As demonstrated in the present study, European flat oyster beds in the northern hemisphere have the potential to deposit more carbon per m^2 than terrestrial forests, in the northern hemisphere through biodeposition alone (Table 2). Oyster beds compare favourably with other shellfish habitats but probably deposit less carbon per m^2 than marine habitats dominated by primary producers (Table 2). Only by considering all sources of carbon deposition (calcification and sediment accretion) as well as loss (respiration and calcification) is it possible to determine whether a habitat is a net carbon sink or source (Figure 3) (*cf* Alongi, 2014; Fodrie et al., 2017). Therefore, although the present study demonstrates significant carbon flux to the seabed, without further research focusing on carbon release it is not yet clear if European flat oyster beds are net carbon sinks. In summary, the real-time carbon budget of an oyster bed can be presented as follows (Figure 3):

Eq 2. Net carbon deposition = (Biodeposition + passive sedimentation + Calcification) – (Respiration CO_2 + Calcification CO_2)

Elsewhere, Lindenbaum et al. (2008) demonstrated that similar shellfish beds formed by *M. modiolus* off Pen Llŷn (North Wales) had a historical vertical build-up of up to 2 metres of deposits. Kent et al. (2017) subsequently estimated that this 373 ha bed would have 1.87 million m^3 of associated deposited sediments stored in it. This build up would be both sediment and shell and therefore studies of carbon budgets must consider both components. Overall, six factors must be quantified to facilitate assessment of whether a carbon budget equates to ‘sink’ or ‘source’ status (Ullman et al., 2013) and many of these are not yet considered in bivalve habitats:

- Rate at which the ecosystem naturally sequesters carbon
- Stock of sequestered carbon
- Release or extent of carbon released when degraded/disturbed
- Accurate measurement of changes in sequestration or emission
- Areal extent, latitudinal variation and temporal change
- Natural variation and anthropogenic triggered variation

The net carbon store budget is therefore:

Eq 3. Net carbon store = Net carbon deposition – (Rate of loss e.g. erosion + resuspension + remineralisation (As presented in Figure 3))

Historically, Scotland’s biggest fishery for oysters, which is now extirpated, was in the Firth of Forth. At the peak of the fishery in the 1800s, the beds covered 31,000 ha and at least 3,000,000 oysters per annum are known to have been extracted for a decade (Thurstan et al., 2013). Using the sediment (TPM) and carbon (CHN analysis) deposition values measured in the present study, it is possible to hind-cast that the harvested oysters (3,000,000 annum^{-1}) would have deposited ~ 38 tonnes of sediment year $^{-1}$ equating to ~975kg IOC year $^{-1}$ and ~1790kg OC year $^{-1}$. The oyster population size of the Firth of Forth bed at its peak is unknown (Thorngren et al., 2013); only through developing a baseline understanding of what the density of an extensive self-sustaining oyster population may have been (*cf* Pauly, 1995), is it possible to estimate its ecological function. Overall, dependent on bed density the Firth of Forth oyster beds may have deposited between 790t and 197kt of sediment per annum through active deposition (Table 3). This rationale can also be applied to the restoration target of 4,000,000 oysters for the Dornoch Environmental Enhancement Project (see Fariñas-Franco et al., 2018) where deposition of ~ 51 tonnes of sediment year^{-1} might therefore be expected, containing ~1299kg IOC and ~2386 kg OC. Scaling in such a way is a potentially useful tool for quantification of potential ESS provisioning expected as a result of habitat restoration.

In the context of marine management for climate change mitigation, without fully understanding the carbon budget, and sequestration and erosion rates of a blue carbon store it would be difficult to i) account for carbon accretion of the store as a mitigation tool and ii) determine resilience to disturbance (Herr et al., 2017; Ullman et al., 2013). The use of habitat protection to reduce marine habitat degradation should be considered as a mechanism to avoid further carbon emissions and allow carbon sequestering habitats to recover (Miteva, Murray & Pattanayak, 2015). However, by only protecting a blue carbon store, climate change cannot be mitigated actively. To actively mitigate climate change, the management of a blue carbon store should consider both the conservation and recovery of these habitats as well as their restoration to increase current sequestration rates to a natural or higher than natural level (e.g. Howard et al., 2017; Lotze et al., 2006; Taillardat, Friess & Lupascu, 2018).

It has been common practice to use LOI as a measure of carbon. However, this study demonstrates that using LOI to predict carbon content without relevant quantification of carbon through CHN analysis (to both region and habitat type) can be problematic. TOM content was observed to be eighteen times greater in the present study than OC content. Quantification of carbon through CHN analysis is primarily the most reliable means of estimating sediment carbon ratios as demonstrated herein. Conversion equations formulated by running LOI and CHN analyses in tandem and considering the relationship between these values provide more useful assessment tools when used appropriately (*cf* Howard et al., 2014).

This work presents a snapshot of the carbon deposition of the European flat oyster both spatially and temporally, in a system fed with natural sea water from a specific location at a specific time of year. In a 'natural' oyster bed, further variability in benthopelagic coupling would be expected as a result of differences in, for example, food availability, seasonality and community processes such as bioturbation. Further work is required to understand the effects of factors such as the potential for density effect (Widdows et al., 2002) and the effects of seasonality and food availability on feeding behaviour and consequently deposition rate (Cranford et al., 2011; Kent et al., 2017b; Navarro & Thompson, 1997). The present study was conducted before the seasonal plankton bloom and before sea water temperatures increased over the summer, therefore the extrapolated biodepositional rates presented here are likely to be conservative estimates (*cf* Haven & Morales – Alamo, 1966; Kent et al., 2017b; Levinton & Doall, 2019; Navarro & Thompson, 1997; Tsuchiya, 1980). Finally, this work considers deposition of carbon in sediments but not loss of carbon through the various pathways (e.g. respiration and calcification) (Alongi, 2014; Herr et al., 2017; Ullman et al., 2013; Figure 3).

Quantification of active deposition of the European oyster provides a valuable tool for beginning to approximate ESS provision by a once abundant species which is now the focus of international restoration work. Policy makers, restoration funders and marine spatial planners all benefit from tangible evidence of ESS provision. Such evidence is key when determining the value of habitat restoration and how once overlooked carbon capturing habitats may be integrated into the management of blue carbon with the aim of both protecting the carbon stores and enhancing accretion rates.

Conflicts of interest statement

The authors confirm that they have no conflicts of interest to declare in relation to this submission

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Tables

Table 1. Deposition rates of total particulate matter (TPM), total organic matter (TOM), total inorganic matter (TIM), organic carbon (OC) and inorganic carbon (IOC) expressed in g m^{-2} day^{-1} and % deposition of TPM for a density of 75 oyster m^{-2}. Data for three groups (‘live’, ‘dead’ and control) are presented.

Treatment	TPM	TOM	TIM	OC	IOC
g m^{-2} day^{-1}					
Live	2.62 ± 0.57	0.56 ± 0.16	0.13 ± 0.03	0.14 ± 0.05	0.06 ± 0.06
Dead	0.95 ± 0.30	0.14 ± 0.02	0.05 ± 0.02	0.03 ± 0.01	0.02 ± 0.01
Control	0.91 ± 0.28	0.15 ± 0.06	0.07 ± 0.05	0.04 ± 0.01	0.02 ± 0.02
% proportion of TPM					
Live		21.3 ± 3.11	5.2 ± 1.04	5.36 ± 1.12	2.34 ± 1.27
Dead		14.84 ± 2.39	5.9 ± 3.38	4.67 ± 1.27	2.37 ± 0.96
Control		16.4 ± 1.75	7.9 ± 3.05	4.02 ± 1.20	2.94 ± 0.97

Table 2. Annual values of carbon deposition defined as sedimentary, carbonate or sedimentary + carbonate per ecosystem. +? Indicates data deficiency.

Ecosystem	Carbon store type	Carbon deposition per annum (g m^{-2})	Source
Seagrass	Sedimentary	83	Duarte, Middelburg & Caraco (2005)
Saltmarsh	Sedimentary	210	Chmura, Anisfeld, Cahoon, & Lunch (2003)
Mangroves	Sedimentary	174	Alongi (2014)
Maerl	Carbonate	74	Burrows et al. (2014)
Horse mussel (density 40 m^{-2})	Carbonate (+?sedimentary)	40 (+ ~ 360 OM deposition†)	Collins (1986); Kent et al. (2017b)
Oyster (density 75m^{-2})	Sedimentary (+?carbonate)	50	Present study
Terrestrial Forests‡	Net sink	29	Pan et al. (2011)

†data is available on organic content of sediment deposits rather than carbon deposition

‡Net global sink/global forest cover

Table 3. Scaling of predicted deposition of total particulate matter (TPM), inorganic carbonate carbon (IOC) and organic carbon (OC) for the expatriated Firth of Forth oyster bed at different bed densities.

Density (m^{-2})	Est. population	TPM	IOC	OC	Density source
0.2	6.2×10^{-7}	790t	20t	37t	Cooke, 2003
3.5	10.85×10^{-8}	14kt	352t	647t	University Marine Biological Station Millport, 2007
5	1.5×10^{-9}	20kt	503t	925t	Thorngren et al., 2019
50	1.5×10^{-10}	197kt	5kt	9kt	Tully & Clarke, 2012

Figure legends

Figure 1. Experimental set-up showing inflow, outflow, baffles, air stones, table (dashed rectangle) and experimental unit configuration. Oyster image by SGW Illustrations.

Figure 2. Deposition rate of the native oyster (mean ±SD) presented as either gm^{-2} day^{-1} or % proportion of total particulate matter deposition (TPM) a) mean TPM, b) mean total organic matter deposition (TOM) c) mean total organic matter (TOM) content expressed as a percentage of TPM deposition (gm^{-2} day^{-1}), d) mean total inorganic matter deposition (TIM), e) mean total organic carbon (OC) deposition. Bottom right depicts experimental units, dashed surface depicts scouring pad. Oyster image by SGW Illustrations. Non-significance is denoted by a shared letter ($p > 0.05$).

Figure 3. Conceptual carbon budget of European flat oysters. Directionality of arrows indicates carbon deposition (downward) or carbon release (upward), arrow size gives qualitative indication of relative size of carbon flow. Oyster image by SGW Illustrations.

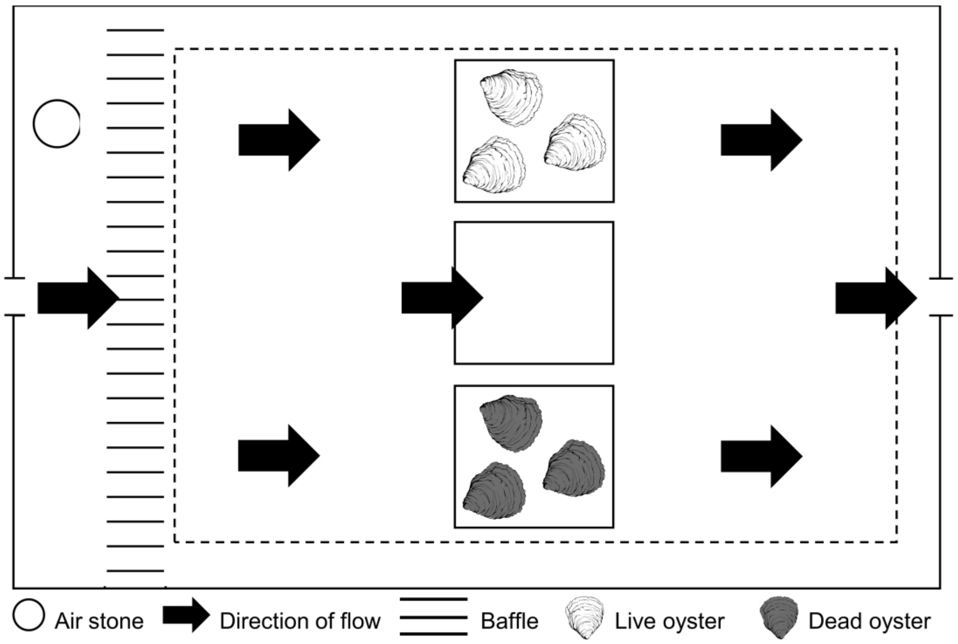

Figure 1. Experimental set-up showing inflow, outflow, baffles, air stones, table (dashed rectangle) and experimental unit configuration. Oyster image by SGW Illustrations.

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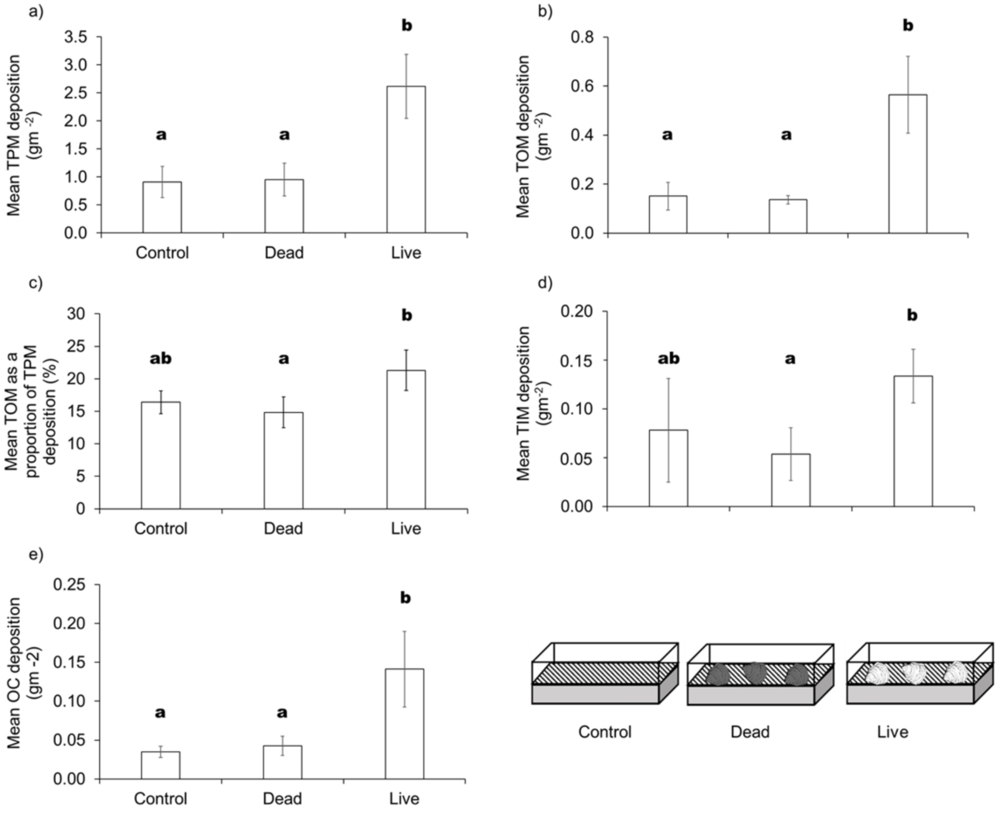

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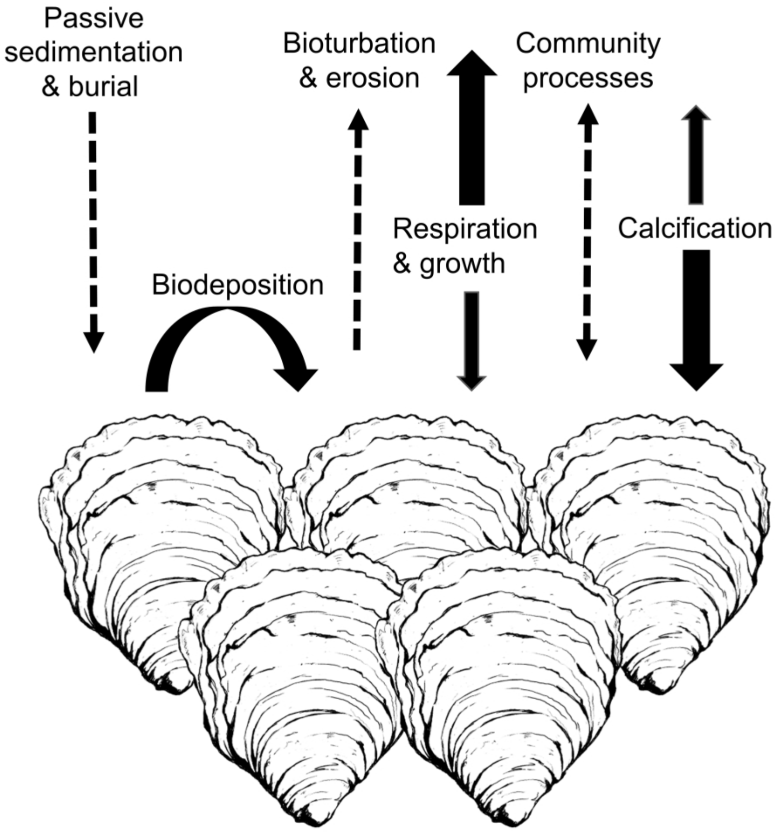

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