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A blue carbon model for the European flat oyster (*Ostrea edulis*) and its application in environmental restoration

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Abstract

- Historically, considerations of the carbon budget of bivalve shellfish have disproportionately focused on the cycling of carbon in shell alone, overlooking respiratory release and the potential role of bivalve shellfish habitats in the stabilization of sediment, and therefore of carbon.
- Data on carbon cycling are key to providing essential evidence to inform evaluation of management strategies and the business case for restoration of European flat oyster (*Ostrea edulis*) habitats. The purpose of this study was to examine the flat oyster carbon budget at the scale of the individual and to set out a framework to enable future comparisons of carbon budgets between ecosystems.
- Through the combination of previously established work with measurements of calcification and respiration both *in situ* and *ex situ*, a carbon budget at the scale of a single oyster was determined.
- In consideration of the flat oyster carbon budget, the inclusion of the deposition of sedimentary carbon, as well as carbon stored in shell, balanced with the release of carbon through respiration and calcification suggests that these habitats are unlikely to be significant carbon sinks in the context of global climate change mitigation. However, the recovery of flat oyster beds is likely to facilitate the accretion of substantial carbon stocks that are nevertheless important in conservation management.

KEYWORDS

blue carbon, carbon budget, ecosystem services, European flat oyster, management, restoration

1 | INTRODUCTION

There is increasing recognition amongst global political and industrial leaders that there is a need to mitigate carbon emissions and anthropogenic climate change (UNESCO-IOC, 2021; UNFCCC, 2021). As such, ecological restoration is rapidly gaining recognition and popularity, as an essential element of mitigating the climate and

ecological crisis (UNFCCC, 2021). Marine ecosystems provide a wide range of regulating and provisioning services, including food, water filtration, storm protection, carbon storage, and climate regulation. Understanding the scale of the provision of these services is necessary to efficiently implement restorative conservation management and marine spatial planning (Herr et al., 2017; Lindegren et al., 2018; Strassburg et al., 2020; zu Ermgassen et al., 2020a;

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Mandle et al., 2021; Sea, Hillman, & Thrush, 2022). The expectation is that the restoration of marine habitats and subsequent recovery of ecosystem services will enhance climate resilience of nature and society (Duarte et al., 2013; Macreadie et al., 2021; Schleussner et al., 2021).

One such example of habitat restoration is that of the European flat oyster (*Ostrea edulis*, hereafter referred to as flat oyster). Flat oyster populations have been extensively depleted across their natural range, largely due to historical overfishing (Laing, Walker & Areal, 2006; Thurstan et al., 2013). Since 2013, there has been a rapid increase in flat oyster restoration projects (now more than 30) in response to the severely degraded or depleted status of the species (zu Ermgassen et al., 2020b). The common goal of these projects is not only species recovery, but also the enhancement of the ecosystem services and benefits facilitated by the presence of the biogenic reefs formed by this species (zu Ermgassen et al., 2020a; zu Ermgassen et al., 2020b). Data relating to the scale of ecosystem service delivery can be used as leverage in restoration investment (Grabowski et al., 2012; Callihan et al., 2016; zu Ermgassen et al., 2020a). Improving the efficiency of restoration methods (Preston et al., 2021; Xu & Liu, 2022) is also a powerful mechanism for driving funding for restoration projects (Grabowski et al., 2012; Endsor, Debney & Withers, 2020).

Evidence of ecosystem service benefits, such as improvement of water quality, provision of nursery habitat, and support of fisheries, is well established for a number of bivalve shellfish species that exhibit biogenic reef building (Kent et al., 2016; Kent et al., 2017a; Kent et al., 2017b; zu Ermgassen et al., 2020a). However, significant gaps in our understanding of the ecosystem service provision by the flat oyster remain (zu Ermgassen et al., 2020a; zu Ermgassen et al., 2020b and references therein). This includes uncertainties regarding the role of flat oyster habitats in the cycling of carbon (Kent et al., 2017a; Lee et al., 2020; zu Ermgassen et al., 2020a).

To appropriately account for the benefits derived through ecosystem service delivery, the establishment of standardized approaches in relation to: (i) collating data on service delivery, (ii) estimating scale of service delivery, and (iii) the comparison of ecosystem delivery between habitats is paramount. Robust evidence of the mechanisms of ecosystem function and service provision will not only address these goals but also further understanding of, and appreciation for, potential risks to habitats (Braat & de Groot, 2012; Ullman, Bilbao-Bastida & Grimsditch, 2013; Hamrick & Gallant, 2017; Herr et al., 2017; Jenkins et al., 2018; VERRA, 2022; Laffoley & Baxter, 2022; Dencer-Brown et al., 2022; ICROA, 2022).

1.1 | Carbon cycling in blue carbon coastal ecosystems

An extensive body of evidence identifies tropical seagrass meadows, mangroves, and temperate saltmarshes as substantial blue carbon sinks (see Macreadie et al., 2021 and references therein). Comparatively, there has been considerably less focus on the role of

other marine ecosystems in cycling carbon (Laffoley, 2020). Although evidence is growing of the role of other marine ecosystems (including biogenic habitats, kelp forests, and fjordic or deep-sea sediments) in capturing, storing, and cycling carbon, it remains comparatively sparse (Macreadie et al., 2019; Turrell, 2020; Hilmi et al., 2021). To support the collection of meaningful data, methods used to assess carbon cycling at the ecosystem level must be standardized (see Howard et al., 2014; Preston et al., 2021). Furthermore, this will enable fair comparison of carbon cycling processes between ecosystems for the purpose of comparing the scale of benefits received.

To understand the overall process of carbon sequestration in marine ecosystems, the pathways of carbon cycling should firstly be identified (Nelleman et al., 2009; Alongi, 2014; Hill et al., 2015). The quantification of these pathways and an understanding of the scale of carbon cycling, and the factors that influence it, provide a structure for developing a similar body of evidence as for other marine ecosystems. In vegetated ecosystems (mangroves, saltmarshes, and tropical seagrasses), the balance between photosynthesis and aerobic respiration is considered a key factor in determining sink or source status (McLeod et al., 2011), and photosynthetic activity usually outpaces respiration (Duarte et al., 2013; Alongi, 2014; Howard et al., 2014; Hill et al., 2015). Blue carbon ecosystems are one interconnected component of the much larger global carbon cycle, which includes connectivity between marine ecosystems as well as to the terrestrial environment (Trevathan-Tackett et al., 2015; Duarte, 2017; Smeaton, Austin & Turrell, 2020).

By identifying the different hierarchies within the carbon cycle—for example, global, ecosystem level, local or population level, and the level of the individual organism (i.e. an ecosystem engineer)—it is possible to begin to disentangle how meaningful and standardized measurements of carbon cycling in an individual ecosystem can be made, and this can be presented as a conceptual model (Figure 1). The purpose of this model is to provide a structure to enable components of carbon cycling, at appropriate scales, to be identified and quantified and to then facilitate unbiased comparisons between carbon storage in different ecosystems to be made.

At the fundamental level (Figure 1), the processes relating to an individual organism begins the process of carbon cycling. One specific example of an organism would be a sedentary benthic ecosystem engineer (species that have the ability to ‘[...] modify, maintain and/or create habitat [...]’ or destroy their ecosystems; Altieri, 2021) such as the flat oyster. The organism acts as a ‘processing point’ for carbon, with some processes depositing carbon to the sea bed and others releasing carbon (Alongi, 2014; Hill et al., 2015; Macreadie et al., 2017; Kent et al., 2017a; Lee et al., 2020). Not all carbon accumulated at this level will be retained in the long term (McLeod et al., 2011). The ‘population’ level represents the wider population of the ‘organism’ (e.g. a reef or seagrass meadow) as well as environmental influence over the organism. Synergistic interactions at the ‘population’ level further influence the rates of carbon accumulation and turnover (Widdows & Brinsley, 2002; Schwindt, Iribarne & Isla, 2004), whereas phenotypic variation in population structure and the influence of environment influence metabolic

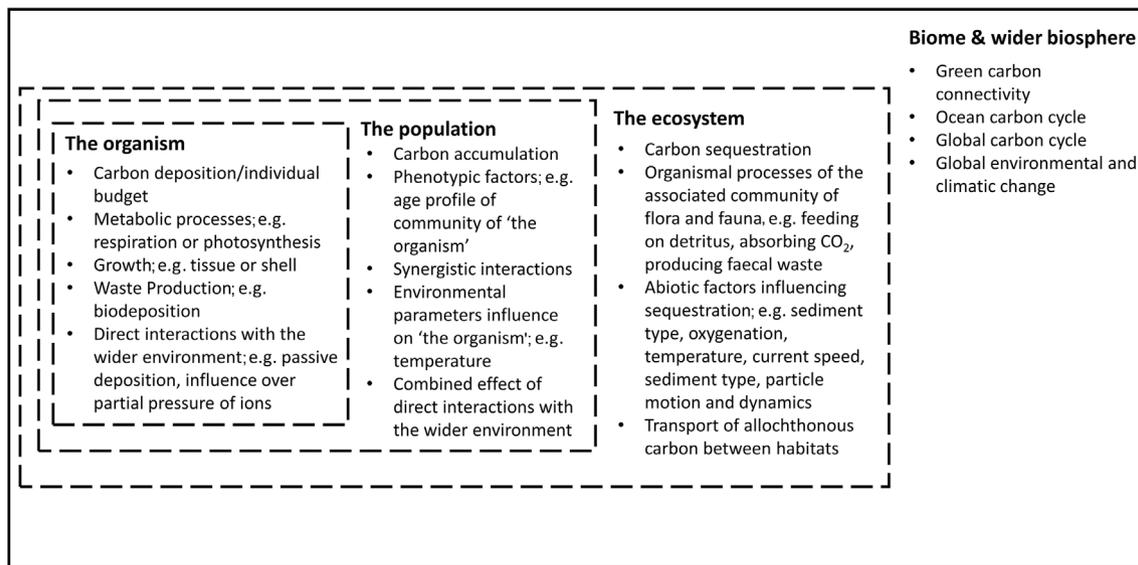


FIGURE 1 Conceptual model depicting the processes supporting carbon sequestration in a blue carbon habitat. Each 'box' represents a defined level at which carbon cycling occurs; levels are nested within each other, and dashed outlines depict interactions between defined levels.

activity of the individual 'organism'; for example, temperature or hydrodynamics (Grizzle, Langan & Howell, 1992; Kittner & Riisgård, 2005).

At the 'ecosystem' level (Figure 1), biotic and abiotic factors will have direct influence on carbon sequestration; for example, carbon retention, resuspension, and rates of carbon degradation (Hedges & Keil, 1995; Schaffner et al., 2001; Nelleman et al., 2009; Keil, 2017). Organismal processes throughout the wider associated community of flora and fauna will influence the overall carbon budget of the ecosystem (Kristensen et al., 2012; Alongi, 2014; Kauppi et al., 2018), and connectivity and proximity to other habitats will dictate the scale of input of allochthonous carbon (Duarte et al., 2013).

Beyond this point, the wider connectivity of the ecosystem to the local 'biome and larger biosphere' (Figure 1) has an overarching influence on habitat function and service provision (Houghton, 2003; Nelleman et al., 2009; Fodrie et al., 2017; Smale et al., 2018; Macreadie et al., 2021). However, these processes at each 'level' outlined do not happen in isolation and are influenced by processes associated with other 'levels', as indicated by dashed boundaries in Figure 1.

1.2 | Carbon budgets in bivalve shellfish habitats

In the context of bivalve shellfish habitats, the 'organism', in the model (Figure 1) would be the individual bivalve and the 'population' would be a reef of bivalves. The reef 'ecosystem' includes the other associated organisms; and finally, interactions with the 'wider biosphere' include multiple interconnected habitats and the wider global carbon cycle. Bivalve shellfish facilitate both the active and passive deposition of carbon, while also releasing carbon through metabolic processes and growth of shell (Fodrie et al., 2017; Kent

et al., 2017a; Lee et al., 2020; van der Schatte Olivier et al., 2020). Through feeding, bivalve shellfish transport suspended particulate carbon to the sea floor (Kent et al., 2017a; Lee et al., 2020). However, the role of calcification has been a primary focus in the consideration of bivalve shellfish beds as blue carbon habitats (Fodrie et al., 2017; Macreadie et al., 2017; Lee et al., 2020; Sea, Hillman & Thrush, 2022). Calcium carbonate (CaCO₃) production can be considered a carbon dioxide (CO₂) source as well as a sink (Frankignoulle, Canon & Gattuso, 1994; Zeebe & Wolf-Gladrow, 2001) because it releases approximately 0.6 mol CO₂ in the process of precipitating 1 mol CaCO₃ (Frankignoulle, Canon & Gattuso, 1994). This occurs as a result of changing the buffering capacity of sea water to CO₂, as the process of calcification in the ocean increases pCO₂ (by reducing total alkalinity through the depletion of carbonate ions; Macreadie et al., 2017 and references therein). Uncertainties still remain as to the fate of this CO₂ (Macreadie et al., 2017 and references therein), and as to whether the processes encompassed by calcification outweigh the accretion and sequestration of carbon in sediments and shell (Fodrie et al., 2017; Howard et al., 2018; Saderne et al., 2019; Lee et al., 2020). Typically, calcification is therefore considered as a net atmospheric source of CO₂. However, this assumes dispersal of CO₂ into the wider marine environment, and subsequently into the atmosphere (Nelleman et al., 2009; Macreadie et al., 2017).

At the 'ecosystem' level (Figure 1), the relationship between calcifying organisms and productivity of the wider associated flora and fauna (e.g. metabolic processes of associated flora and fauna) may offset a proportion of the CO₂ produced (Ware, Smith & Reaka-Kudla, 1992; Fodrie et al., 2017; Macreadie et al., 2017). Timescales are important. Inorganic carbon is considerably less labile than organic carbon—with CaCO₃ shells persisting over centuries to millennia (Macreadie et al., 2017; Fariñas-Franco et al., 2018). To fully

understand carbon cycling in bivalve shellfish beds, both the process of carbon deposition (through calcification and sediment deposition—both passive and active) and release (through respiration and the process of calcification) must be accounted for at the level of the individual oyster. In turn, a more comprehensive account of carbon cycling processes will facilitate more reliable predictions relating to carbon storage capabilities through the recovery of flat oyster habitats.

1.3 | Aims and objectives

The aim of the present study was to estimate the overall carbon budget (Figure 1, 'organism' level) for the European flat oyster (*O. edulis*) for the first time. The objective was to use these data to indicate whether the restoration of flat oyster beds is likely to form carbon sinks. Shell growth, respiration, and calcification were examined through *ex situ* incubation studies emulating natural conditions and the recovery and analysis of samples of oysters growing *in situ*. The study then set out to combine these data with previous measures by the authors of deposition of carbon in sediments through filtration and biodeposition by flat oysters (Lee et al., 2020). The results are discussed in the context of ecosystem benefits that support habitat management.

2 | MATERIALS AND METHODS

2.1 | Annual calcification rate of European flat oysters

Live oysters were collected by scuba divers from the Dornoch Firth (north-east Scotland) from licensed restoration sites as part of the Dornoch Environmental Enhancement Project (DEEP) routine site monitoring.

Samples were retrieved at the time when oysters (aged ~15 months) were first deployed in September 2018 and during subsequent annual surveys in September 2019, 2020, and 2021. Water temperature and salinity at the site were recorded using HOBOware loggers (model U24-002-C) at the Dornoch Firth restoration site between November 2019 and March 2020. Average water temperature in this period was 6.6°C ($SD = \pm 0.8^\circ\text{C}$), average salinity was 24.3 ppt ($SD = \pm 0.5$ ppt).

Recovered samples were frozen at -20°C prior to dissection. Oyster shells were gently scraped clean of encrusting barnacles and keel worms. Total weight was measured to 0.0001 g with an analytical balance, and shell height (SH), shell length, and shell width were measured to 0.1 mm with vernier callipers (Figure 2). Oyster flesh was removed and both valves then dried at 60°C for 48 h before dry shell weight (DSW) was recorded. Once shells were dry, carbon content of shells was determined through acid digestion (Howard et al., 2014; Preston et al., 2021). Annual shell accretion was determined by comparison of average annual size and weight increase.

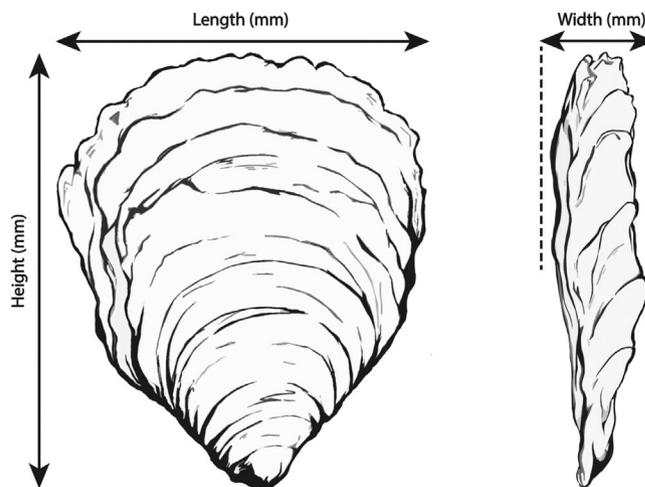


FIGURE 2 Oyster measurements: shell height, shell length, and total shell width. Oyster image by SGW Illustrations, based on zu Ermgassen et al. (2021).

2.2 | Quantifying immersed respiration rates

Quantification of immersed respiration rates was conducted at St Abbs Marine Station (south-east Scotland) between April 23 and 25, 2019. Three repeat incubation experiments (see Tagliarolo et al., 2012) were undertaken in 900 ml chambers covered in black felt to prevent photosynthesis. Chambers were attached to a series of pumps with valves that could be turned on and off to enable water flow through the chamber when experiments were not underway.

Oysters were acclimated in chambers for 7 days prior to incubation experiments and fed with flow-through natural sea water. Chambers were immersed in a larger tank of running sea water to keep them at the ambient sea temperature. Seawater temperature ($^\circ\text{C}$), dissolved oxygen levels (mg L^{-1}), and salinity (ppt) were recorded three times daily (morning, midday, and evening) using a Pro DSS logger (YSI Inc., Yellow Springs, OH, USA).

During incubation experiments the ambient seawater temperature was 8.3°C ($SD = \pm 0.7^\circ\text{C}$), salinity 34.3 ppt ($SD = \pm 0.1$ ppt) and dissolved oxygen of 9.5 mg L^{-1} ($SD = \pm 0.3 \text{ mg L}^{-1}$).

To enable calculation of background changes in dissolved inorganic carbon levels (see Tagliarolo et al., 2012), four chambers held one oyster each, and four 'empty' control chambers held none (filled with sea water but no oyster). Mature oysters of similar size were used (mean average plus/minus SD : height, $74.8 \text{ mm} \pm 0.26 \text{ mm}$; length, $68.3 \text{ mm} \pm 0.16 \text{ mm}$; width, $17 \text{ mm} \pm 0.06 \text{ mm}$; wet weight, $57.25 \text{ g} \pm 8.65 \text{ g}$; dry tissue weight, $3.1 \text{ g} \pm 0.6 \text{ g}$).

Water samples were taken before (T_0) and after incubation (T_1) and preserved prior to analysis (Tagliarolo et al., 2012). Following T_0 water sampling, chambers were sealed at mid-flood tide and incubated for 6 h, after which T_1 water samples were taken. Incubations were repeated on three consecutive days. Following the incubations, the oysters were dissected and tissue wet weight recorded. Tissue samples were dried for 48 h at 60°C and tissue dry weight (DW) recorded.

2.2.1 | Calculating net respiration rate

Dissolved total inorganic carbon (DIC) in water samples was determined through coulometric titration (carbon dioxide coulometer; UIC Inc., Joliet, IL, USA). Subsamples of 10 ml were analysed, as outlined in Dickson, Sabine & Christian (2007). Dickson seawater standard was used as reference material to ensure machine calibration (UCSD/SIO, La Jolla, CA, USA).

Net respiration rates R were calculated as in Equation (1) (Tagliarolo et al., 2012); net respiration rate was then normalized to tissue DW for calculation of net carbon budgets:

$$R \left(\text{g}^{-1} \text{DW h}^{-1} \right) = - \left(\frac{\text{Blank-corrected } \Delta \text{DIC}}{\Delta T} \frac{V}{\text{TDW}} \right) - \text{Net calcification} \quad (1)$$

where V (L) is the total unit volume, TDW (g) is tissue DW, ΔT (h) is the incubation time, and ΔDIC ($\mu\text{mol DIC L}^{-1}$) is the change in DIC.

2.3 | Statistical analysis

All statistical analyses were undertaken in R Studio (R Core team, Version 3.6.3). Data were tested for normality (Shapiro–Wilk test) and homogeneity of variance (Levene's test). A Kruskal–Wallis test was used to investigate whether CaCO_3 content of shell between age classes differed (for samples collected from Dornoch Firth deployments).

The von Bertalanffy growth function (VBGF) parameters were estimated for both SH (SH_∞ (mm), K (year^{-1})) and DSW (DSW_∞ (g), K (year^{-1})).

The height–DSW relationship of the oysters from Dornoch Firth was calculated using the following equation:

$$\text{DSW} = a\text{SH}^b$$

where DSW units are grams, SH units are centimetres, a is the intercept, and b is the slope.

3 | RESULTS

3.1 | Shell growth in the Dornoch Firth

The VBGF parameters for SH at age were $\text{SH}_\infty = 79.62$ mm and an instantaneous growth constant K of 0.83 year^{-1} (Figure 3a). The VBGF parameters for DSW at age resulted in a DSW infinity value of 87.22 g and an instantaneous growth constant K of 0.21 year^{-1} (Figure 3b).

Model outputs for flat oyster in the Dornoch Firth suggest that increases in SH slows down from approximately year 4 onwards. However, as age continues to increase there is a transition between oysters accreting shell as height to accreting shell as weight (i.e. thickening).

No significant differences were observed in shell CaCO_3 content between age groups (Kruskal–Wallis analysis of variance by ranks H (3) = 6.0055, $P = 0.11$), suggesting that, although growth rates may be higher in smaller oysters (Figure 3), shell composition remains constant. The average CaCO_3 content was 92.16% ($SD = \pm 5.92\%$); that is, the average carbon concentration in shell as CaCO_3 was 11.08% ($SD = \pm 0.71\%$).

3.2 | Respiration

The average respiration rate was $5.17 \mu\text{mol DIC g}^{-1} \text{ DW h}^{-1}$ ($SD = \pm 3.6817 \mu\text{mol DIC g}^{-1} \text{ DW h}^{-1}$); that is, $0.0052 \text{ mmol DIC g}^{-1} \text{ DW h}^{-1}$ ($SD = \pm 0.004 \text{ mmol DIC g}^{-1} \text{ DW h}^{-1}$) or $6.21 \times 10^{-5} \text{ g DIC g}^{-1} \text{ h}^{-1}$ ($SD = \pm 4.42 \times 10^{-5} \text{ g C DIC g}^{-1} \text{ h}^{-1}$). This was then scaled to a daily and then an annual respiration rate (Table 1). Though respiration rates for the individual oysters appeared relatively consistent, high variability was observed between oysters, resulting in high variance of the mean.

3.3 | Flat oyster carbon budget

Combining the results of the present study with that of Lee et al. (2020) enables the calculation of a flat oyster carbon budget which

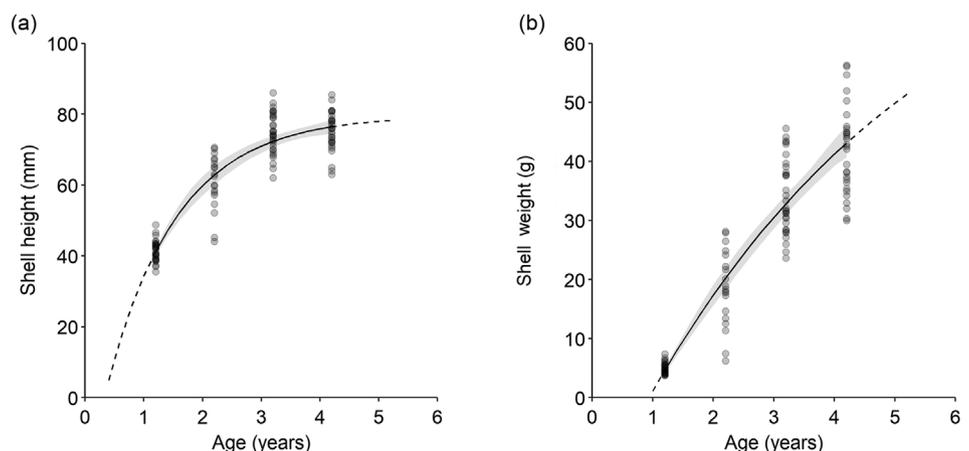
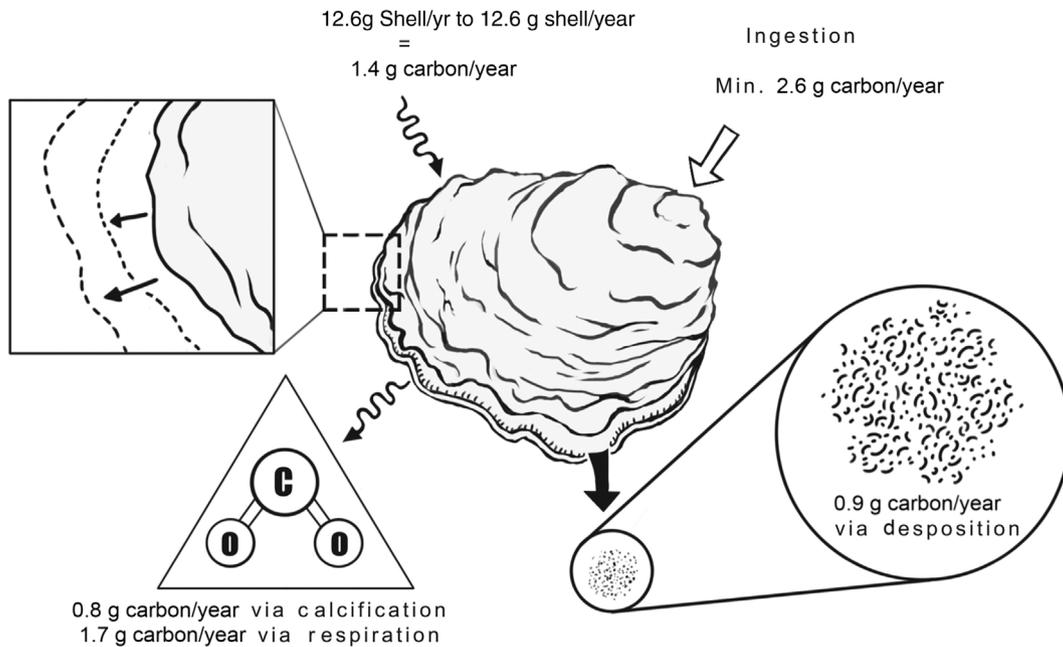


FIGURE 3 Growth rates of the flat oyster *Ostrea edulis* in the Dornoch Firth (2018–2021) presented as (a) shell height at age growth curve and (b) dry shell weight at age growth curve modelled using the von Bertalanffy growth function in R Studio.

TABLE 1 Summary of measurements of carbon included in the carbon budget calculations.

	Estimated intake of carbon	Biodeposition (deposition) ^a	Calcification (deposition) ^b	Respiration (release) ^b	Calcification (release) ^b
Individual oyster per day	7.5 mg (±1.6 mg)	2.5 mg (±0.8 mg)	Measured as per year	4.6 mg (±0.3 mg)	Measured as per year
Individual oyster per year	2.6 g (±0.6 g)	0.9 g (±0.3 g)	1.4 g (±0.3 g)	1.7 g (±1.2 g)	0.8 g (±0.2 g)

^aLee et al. (2020).^bCurrent study.**FIGURE 4** Summary figure of the European flat oyster *Ostrea edulis* carbon cycle, accounting for biodeposition, calcification, and respiration. Illustrated by SGW Illustrations.

takes account of the major pathways of carbon deposition and carbon release (summary presented in Table 1). On average, the annual increase in DSW per oyster was 12.6 g ($SD = \pm 2.3$ g) of which 11.08% ($SD = \pm 0.71\%$) or 1.4 g ($SD = \pm 0.3$ g) was estimated to be carbon (Table 1). The process of calcification is understood to release approximately 0.6 mol CO_2 during the precipitation of every 1 mol carbon bound in shell (Frankignoulle, Canon & Gattuso, 1994; Howard et al., 2014). Per oyster, this would be approximately 0.8 g ($SD = \pm 0.2$ g) of carbon in the form of CO_2 and a net storage of carbon as shell of 0.6 g (Table 1). Average annual release of carbon through respiration was calculated as 1.7 g ($SD = \pm 1.20$ g) of carbon in the form of CO_2 . Previous estimates of transport of carbon through biodeposition resulting from feeding was 34.9 mg total particulate matter per oyster per day, including 2.5 mg carbon per oyster per day (Lee et al., 2020). Annual deposition per oyster is therefore approximately 0.9 g ($SD = \pm 0.3$ g) of carbon as biodeposits.

Intake of carbon from the water column through feeding (ingested carbon) would be, as a minimum, equivalent to biodeposition (of faeces and pseudofaeces) plus carbon respired (2.6 g ($SD = \pm 0.6$ g) carbon per year per oyster; Table 1, Figure 4). However, carbon stored as tissue is not accounted for, as it is unlikely

to be stored beyond the lifetime of the flat oyster. Carbon deposition through passive planktonic deposition (as a result of an increase in rugosity of the sea bed, which would result in an increase in the accumulation of sediment; see Kent et al., 2017a) was not observed in Lee et al. (2020) and is therefore not accounted for in the following carbon budget. Additionally, the value presented does not consider variation as a result of changing seasonal temperatures, food availability, or size and age of oyster. The individual flat oyster carbon budget (for oysters of the size presented here) can therefore be calculated (Equation (2); adapted from Lee et al., 2020) as follows:

$$\text{Net carbon deposition} = (\text{Ingested carbon} + \text{Calcification}) - (\text{Respiration as } CO_2 + \text{Calcification as } CO_2) \quad (2)$$

Therefore, the annual carbon budget for an oyster can be estimated as (Equation (3), summarized in Figure 4)

$$(2.6 + 1.4) - (1.7 + 0.8) = 1.5 \text{ g } (SD = \pm 0.8 \text{ g}) \quad \text{deposition of carbon per oyster per year to the sea bed} \quad (3)$$

4 | DISCUSSION

Drawing on the conceptual model presented in Figure 1, this study set out to estimate the overall carbon budget and estimate net carbon deposition of the individual flat oyster. The flat oyster is essentially a processing unit, feeding and respiring, transporting, and 'repackaging' carbon to tissue, shell, and biodeposits. This study indicates that the net carbon budget in the context of the flat oyster is not likely to offer a carbon sink comparable to that of saltmarshes or mangroves. This study instead suggests that habitats created by the flat oyster are likely to store carbon as shell and sediment on the sea bed and thereby stabilize it, especially in protected areas. Understanding the role of priority habitats in provision of ecosystem services directly supports implementing conservation and management objectives.

The conceptual model (Figure 1) enables the data presented herein to be considered in different contexts and the implications and limitations of this study to be outlined. At an organismal level the carbon in tissue was not accounted for in the flat oyster carbon budget presented. Others have considered carbon and nutrient removal through mariculture where tissue is removed through harvest (van der Schatte Olivier et al., 2020). Although tissue may contribute to overall carbon burial as 'biomass carbon' (Lutz & Martin, 2014) within the flat oyster habitat when the animal dies, ultimately, a significant proportion of flat oyster biomass is likely to be metabolized by predators and scavenging crustaceans and whelks (Lee, personal observation). Thus, the wider fate of tissue carbon within the flat oyster habitat is unclear (see Saba et al., 2021; Nowicki, DeVries & Siegel, 2022). Furthermore, the present study predicts approximately 2.5 g carbon per flat oyster would be released through respiration and as a result of the process of calcification annually. However, the study cannot conclude the fate of this carbon; that is, it is not necessarily released into the atmosphere; instead, this carbon may be absorbed by the associated species in the ecosystem (Figure 1 the 'ecosystem' and Figure 4; also see Macreadie et al., 2017). A deeper understanding of the interactions (dashed lines within the model in Figure 1) between individual flat oysters and with the wider associated species assemblage is clearly still required, and further studies may consider the inclusion of tissue carbon, specific analysis of carbon in the food taken up, or the cycling of dissolved organic carbon in more detail (e.g. Bertolini, Pastres & Brigolin, 2023).

Components of the flat oyster carbon budget would also be expected to fluctuate both spatially and temporally (Figure 1). Repetition of the current study at both a geographical and temporal level would increase the evidence available for drawing conclusions regarding flat oyster carbon budgets at larger, regional levels. Such estimates would provide essential evidence to regionally restricted flat oyster restoration projects that would support planning and delivery of restoration goals relating to ecosystem service provisioning (see zu Ermgassen et al., 2020a). Changes in physical oceanographic parameters, availability of food, and population age are all known drivers of variability for metabolism, growth, and waste production in marine bivalves (see Lee et al., 2020 and references

therein). In the present study, the rate of change in calcification, respiration, and biodeposition are likely to be proportional. For example, increasing seasonal food availability with the summer plankton bloom would be expected to elicit a physiological response (Hawkins & Bayne, 1984; Marescaux et al., 2016). Thus, feeding, and therefore biodeposition rate, would be expected to increase (Rahman et al., 2020), as would metabolic activity and an increase in growth rate coupled with respiration. Others have noted that physical oceanographic parameters can elicit an interconnected physiological response in bivalves (Walne, 1974; Grizzle, Langan & Howell, 1992; Cranford, Ward & Shumway, 2011). Therefore, any seasonal variation in the rates reported here would be unlikely to dramatically change the overall balance of the carbon budget at the level of the 'organism'. Dependent on the site characteristics, variability in maximum size-at-age of flat oysters is also to be expected (see Fariñas-Franco et al., 2014; Brash et al., 2018). Sites where growth rates are higher will probably result in larger flat oysters and greater stores of carbon (see Burrows et al., 2014).

At the 'population' level, synergistic interactions, such as the hydrodynamic influence of aggregations of bivalve shellfish on passive deposition or feeding behaviour (see Widdows & Brinsley, 2002; Kent et al., 2017a; Lee et al., 2020; Lim, Fraser & Knights, 2020; Sansom et al., 2020), would likely increase the scale of carbon deposition. This study predicts carbon cycling at the level of the individual flat oyster and supports a first estimate of how much carbon could be accreting in a habitat. Beyond these predictions, further understanding of the stability of accreted sediments would enable more accurate estimates to be made of long-term carbon storage. Stabilization of sediments directly relates to the bivalve shellfish population density (Widdows & Brinsley, 2002) and sediment characteristics (Montserrat et al., 2009). The raised structure of a flat oyster bed would be expected to trap sediment interstitially (see Callaway, 2018) and reduce overall flow rate across the bed (see Widdows & Brinsley, 2002). Subsequently, both resuspension of sediments (reduced) and sediment deposition (increased) would be influenced by the structure of the living flat oyster bed, particularly in comparison with habitat where no biogenic bed or reef is present (Styles, 2015; Kitsikoudis, Kibler & Walters, 2020).

At an 'ecosystem' level, secondary production, respiration, and excretion by other biota may further contribute to the carbon budget of a flat oyster habitat (Alongi, 2014). Interactions between the flat oysters and the biodiverse community of marine organisms associated with them are likely to further enhance benthic-pelagic coupling, transporting more carbon from sea water to sea bed through feeding and biodeposition (Kent et al., 2017a; Lown et al., 2021; Kennon et al., 2023). While in the photic zone, flat oyster and other bivalve shellfish habitats have been recorded with a substantial algal turf (Fariñas-Franco et al., 2022; Kennon et al., 2023), which will add primary production to the carbon budget at the ecosystem level. In the case of flat oyster beds, an associated algal assemblage could absorb CO₂ produced by the flat oysters before it was released into the atmosphere, though to what extent remains to be determined (Troell et al., 2009; Mcleod et al., 2011).

Additionally, the proximity of flat oyster beds to other blue carbon habitats is relevant at the 'ecosystem' level (Figure 1) because connection to detrital pathways from other habitats (e.g. algal and seagrass fragments) may influence the rates of passive deposition and, therefore, carbon accretion. For example, proximity to low (e.g. sand flats) or high sedimentary carbon habitats (saltmarshes) has been shown to change carbon fluxes in North American oyster beds (Fodrie et al., 2017). Proximity to carbon-rich habitats is also likely to result in enhanced availability of carbon-rich particulate food. In addition to allochthonous sedimentary carbon, bivalve shellfish beds are likely to trap and store shell of non-oyster origin; for example, fragments of *Cerastoderma edulis* or *Mytilus edulis* shell (see Southworth et al., 2010). Looking beyond the individual flat oyster carbon budget, using the values in the present study, it is possible to make predictions regarding the scale of carbon flux within a restored flat oyster bed. These predictions are of carbon accumulation (the 'population' level; Figure 1), rather than overall sequestration (the 'ecosystem' level; Figure 1). Such predictions are likely to be conservative, given the other potential processes discussed earlier, but provide a valuable initial insight into the role of ecosystem-scale restoration in the recovery of ecosystem function and the delivery of ecosystem services.

The Dornoch Environmental Enhancement Project aims to restore 4,000,000 flat oysters; therefore, based on Equation (3) and the present data, that would equate to a net carbon deposition of 6.0 t carbon per year ($SD = \pm 3.0$ t; 22.02 t CO₂ equivalent). Through shell growth and biodeposition, 4,000,000 flat oysters would be expected to facilitate the deposition of approximately 9.3 t (34.1 t CO₂ equivalent) of carbon per year, of which 40% would be in sediment and 60% in shell. Although climate change mitigation cannot yet be claimed for the restoration of flat oyster habitats, a growing body of evidence is demonstrating that bivalve shellfish beds can build up carbon stores over time as both sediment and shell (see Lindenbaum et al., 2008; Kent et al., 2017a; Sea, Hillman & Thrush, 2022), and some bivalve shellfish habitats have been shown to persist for decades, if not centuries (Lindenbaum et al., 2008; Fodrie et al., 2017; Sea, Hillman & Thrush, 2022). Where habitats remain intact, the carbon storage benefits of a living flat oyster bed may also persist beyond the lifetime of the flat oysters themselves (Albertson et al., 2022); as such, minimal disturbance of both extant and relic habitats is likely beneficial to the longevity of a carbon store.

As evidence of the significance of marine habitats in sequestering carbon has increased, so has the focus on the possible impacts of disturbance, degradation, and climate change on these same habitats (Lovelock et al., 2017; Vanderklift et al., 2019; Laffoley & Baxter, 2022). Estimates of carbon flux, such as those presented here, are a first step in understanding the scale of carbon cycling that may occur upon restoration and in turn help to demonstrate the numerous benefits elicited from habitat restoration. However, habitat loss will likely impact climate change mitigation strategies because the disturbed carbon is released back into the environment, creating conditions that favour breakdown of organic matter and the subsequent release of CO₂ (Pendleton et al., 2012; Lovelock

et al., 2017; Macreadie et al., 2019). Further understanding of the true fate of such carbon will enable better future estimates of the influence of habitat disturbance on the release of carbon to be made (see Macreadie et al., 2017; Goldstein et al., 2020). At present, estimates of carbon sequestration in flat oyster habitats are still preliminary and likely to be underestimated; however, they can be used to consider the scale of the risk of the loss of these habitats.

The application of standardized monitoring approaches (see Preston et al., 2021), supported by the conceptual model presented herein, will enable both carbon flux and baseline estimates of carbon storage to be made in flat oyster and other blue carbon habitats. Owing to the lack of extant intact flat oyster beds, direct measurements of carbon storage remain difficult; however, restoration projects should seek to monitor carbon accretion at restoration sites over time. Overall, this study demonstrates the importance of accounting for all components of the carbon budget (shell growth and calcification, deposition, respiration) rather than specific components in isolation (e.g. CaCO₃ deposition) and illustrates the scope to build upon the present understanding of bivalve shellfish habitat benefits to provide evidence to support conservation and restoration project objectives.

AUTHOR CONTRIBUTIONS

Hannah Z. L. Lee: Conceptualization; methodology; investigation; project administration; data curation; formal analysis; visualization; writing—original draft; Validation. **Ian M. Davies:** Writing—review and editing; conceptualization; supervision. **John M. Baxter:** Writing—review and editing; conceptualization; supervision. **Karen Diele:** Writing—review and editing; conceptualization; supervision. **William G. Sanderson:** Writing—review and editing; conceptualization; supervision; funding acquisition; resources.

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CONFLICT OF INTEREST STATEMENT

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

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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