Southern Inshore Fisheries and Conservation Authority

Literature Review of Bivalve Ecosystem Services

Supporting document for the Appropriate Assessment for the Issuing of Leases under The Poole Harbour Fishery Order 2015 for 2025-2030

Contents

Introduction

This literature review aims to present information from peer-reviewed literature and reports on the beneficial ecosystem impacts of shellfish aquaculture in Poole Harbour by considering the potential effects on Marine Protected Area (MPA) features and the broader marine environment through nutrient cycling, including nitrogen, phosphorus, and carbon. Additionally, this literature review explores the natural capital value provided by Poole Harbour aquaculture operations and highlights potential ecosystem services.

Aquaculture in Poole Harbour primarily focuses on three main bivalve groups: Pacific oysters, clams, and mussels, located across 12 lease beds within an 837.8-hectare area outlined in the Poole Harbour Fishery Order 2015. Poole Harbour is an economically active maritime area that fishing vessels, charter vessels, ferries, and recreational water sports share. As a result, bivalve aquaculture in The Harbour is primarily on-bottom where shellfish are laid directly on the seabed without the addition of any structures, allowing aquaculture to take place in a spatially competitive area. The only exception is small-scale off-bottom mussel farming in the form of vertical ropes suspended from already existing structures. The total aquaculture production in Poole Harbour reached 700,000 kg in 2014/15. The total economic activity of aquaculture in Poole, including gross output and indirect output from industries, was estimated to be worth £2,615,250 in 2018 (Williams & Davies, 2018). However, the ecosystem services offered by these farmed bivalves have not been quantified to date.

Ecosystem services

Ecosystem services refer to benefits (in the form of goods and services) that humans derive from a healthy natural environment. Although shellfish are primarily cultivated as a food source, the culturing of organisms will impact the wider marine environment through changes to biochemical cycles and habitat alterations. In turn, any environmental change will influence the communities that depend on them.

1. Nutrient Cycling

1.1. Issues arising from nutrient cycling

- Eutrophication refers to the process of over-enriching waters with nutrients from onshore and offshore human activities. Nitrogen and phosphorus influxes are the most notable and can lead to rapid increases in algae concentrations, altering habitats and ecosystems. The rapid colonisation of algae can lower oxygen levels and has been associated with the deaths of fish and other aquatic organisms, in addition to the decline of key habitats such as seagrass beds.
- Both nitrogen and phosphorus are important for eutrophication cycles however, nitrogen is often the limiting nutrient controlling the process in marine environments (Pedersen & Borum 1996). In Poole Harbour high nitrogen inputs have been attributed to the expansion of green macroalgae *Ulva lactuca* in the form of algae mats (Franklin et al., 2020). Thornton et al. (2020) recorded a significant decrease in invertebrate abundance across the Poole Harbour MPA following the expansion of these algae mats, impacting protected overwintering birds that rely on the biodiversity of intertidal mudflats as feeding grounds.
- Dissolved inorganic nitrogen concentrations are predicted to increase across the Poole Harbour Marine Protected Area over the next 15 years primarily due to offshore run-off from historic fertiliser catchments (Franklin et al., 2020).

1.2. Nutrient removal by commercial bivalve species

- Filter-feeding organisms like bivalves cycle nutrients through benthic-pelagic coupling. Bivalves naturally remove nitrogen and phosphorus from the water column by filtering suspended particles and nutrient-rich plankton. A portion of these nutrients are incorporated into bivalves through shell and tissue growth which can be directly removed from the system during harvesting (Holmer et al., 2015).
- The remaining nutrients are expelled in the form of organically rich biodeposits (in the form of pseudofaeces and faeces), and ammonia to the sediment (Dumbauld et al., 2019) and can be buried in the process of sedimentation or undergo further remineralisation by microbial activity. This material can enhance bacterial denitrification which can help further remove nitrogen from the water column via atmospheric nitrogen (N_2) production.
- The nitrogen and phosphorus content of bivalve tissue is species-dependant and can vary based on the cultivation method and physiochemical conditions (van der Schatte Olivier, 2020).
- The majority of literature surrounding the eutrophication mitigating capacity of bivalves focuses on nitrogen removal as opposed to phosphorous removal due to nitrogen commonly being the limiting nutrient for algae growth in marine systems (Pedersen & Borum, 1996). A recent literature review estimated that 82% of bivalve nutrient removal studies focused on nitrogen, while the remaining 18% investigated both nitrogen and phosphorus removal (Woźniacka, 2024).
- A study by van der Schatte Olivier et al. (2020) valued the nitrogen and phosphorus remediation capacity of European shellfish (Including harvesting and denitrification) in 2015 at $70,459,000 and $10,286,000 respectively.

1.3. Harvest removal estimates

- Laboratory experiments investigating the filtering capacity of blue mussels (*Mytilus edulis*) and Pacific oysters (*Magallana gigas*) found that up to 62% of Poole Harbour could be filtered, depending on tidal factors (Gravestock et al., 2020). A study investigating the filtration rate of the closely related oyster species, *Crassostrea virginica*, found similar filtration levels in Chesapeake Bay (Newell, 1988).
- While the specific nitrogen removal rates for Bivalves in Poole Harbour are scarce, elemental analysis of the nutrient content of eastern oyster (*Crassostrea virginica*) bottom cultures found that oysters cultivated in various eutrophied coastal estuaries had a consistent tissue nitrogen content of 8.6% ± 0.2% (Carmichael et al., 2012).
- European project GAIN has estimated the removal of nitrogen in 2018 for European Union countries and the UK. The estimates based on two methods (proximate analysis and modelling using FARM software) using data on UK *M. edulis* production indicated potential nitrogen removal reaching between 125 tonnes to 248 tonnes per year through tissue growth (Cubillo et al., 2023). Of these bivalves, blue mussels were shown to have the greatest % of nitrogen in live weight (0.88%), followed by Pacific oysters (0.37%), Manila clams (0.32%) and European flat oysters (0.29%).
- Pacific oysters were shown to remove between 8.2 - 19 tonnes of nitrogen per year, and European flat oysters (*Ostrea edulis*) were shown to remove 0.05 – 0.1 tonnes of nitrogen per year across the UK through growth (Cubillo et al., 2023). Additionally, studies investigating nitrogen removal in the Chesapeake Bay found that 7.7 million cultured *M. gigas* oysters removed 1 tonne of nitrogen through tissue growth (Rose et al., 2015).
- Woźniacka (2024) used proximate analysis to investigate the nutrient content of commercially important bivalves in the UK. The analysis was based on the results of the elemental analysis of four commercial bivalve species from the GAIN project (Ferreira, 2020) as well as modelling using FARM software. In accordance with the GAIN project estimates, this work calculated a potential UK removal of between 126 to 362 tonnes of nitrogen in 2019, depending on farming practices and environmental parameters.
- In 2013, when production was higher, the more conservative proximate analysis indicated a removal of over 203 tonnes. By analysing the costs for the Wessex Water treatment facility to

remove nitrogen and applying them UK wide, the FARM model suggests that the removal of 126 t to 362 t of nitrogen could save between £7,000,000 - £21,000,000 annually (Woźniacka, 2024).

- Research by Rose et al. (2015) indicates that the cultivation of *M. gigas* can remove around 23 g m^2 of nitrogen annually in Scotland's Loch Creran and approximately 74 g m^2 in Ireland's Lough Ireland. Furthermore, the average nitrogen removal by *M. edulis* has been estimated to range between 5 and 8.50 kg of nitrogen per tonne using upscaled elemental analysis (van der Schatte Olivier et al., 2021).
- EU/UK-wide nitrogen removal using scaled-up data from 5 European shellfish mariculture sites, including an *M. gigas* bottom culture farm in Scotland, valued UK and EU eutrophication mitigation capacity of shellfish mariculture at a net €11–17 billion annually (Ferreira et al., 2009).
- Analysis of longline *M. edulis* cultivated in areas of high eutrophication found that harvesting farmed mussels removed between 0.6-0.9 t nitrogen ha^{-1} $year^{-1}$ and 0.03-0.005 t phosphorus ha^{-1} $year^{-1}$. In contrast, nitrogen removal in alternative wetland habitats has been measured at 0.1 t Nitrogen ha^{-1} $year^{-1}$ (Petersen et al., 2014), highlighting the potential of bivalve aquaculture as an alternative bioremediation tool. A separate study estimated that every kilogram of commercial shellfish harvested would remove on average, 16.8 g of assimilated nitrogen (Rice, 2001).
- Recent literature regarding bivalve bioremediation studies has primarily focused on mussels and oysters, especially in UK publications (Woźniacka, 2024). *Magallana gigas* have been shown to remove ~10% of the daily nitrogen loadings into north Hiroshima Bay Japan through harvesting. These findings are consistent with studies on oyster and mussel nitrogen removal rates recorded in eastern Canada (Clements & Comeau, 2019).
- However, Manila clams (*Ruditapes philippinarum*) have been recorded removing 28.7% and 43.3% of daily nitrogen and phosphorus loading into Jiaozhou Bay China respectively (Zan et al., 2014). The variability of nitrogen removal rates indicates that it would be beneficial to apply a FARM model to quantify nitrogen removal for Poole Harbour (Gravestock et al., 2020).

1.4. Impacts of the farming method and species

- Cultivation methods can impact food availability and growth, impacting bivalve nutrient removal efficiency. A FARM model of *M. gigas* bottom cultures in Sweden was shown to reduce chlorophyll *a* by 14-82% depending on stocking density (Ferreira et al., 2007).
- A UK estimate found that phosphorus removal in mussels when harvested was more than doubled in suspended cultures (0.95 kg) than bottom cultures (0.43 kg) (van der Schatte Olivier et al., 2021). This was supported by another study that found that rope *M. edulis* cultures in the UK removed significantly more nitrogen and phosphorus through harvesting (8.50 ± 0.59 kg of N, 0.95 ± 0.07 kg of P) than bottom cultivated mussels (5.00 ± 0.013 kg of N, 0.43 ± 0.01 kg of P). This has been attributed to greater tissue growth at the expense of shell growth from suspended aquaculture. Suspended bivalves experience lower predation pressure that reduces the need for stronger shells in favour of tissue growth. Additionally, suspended bivalves, by being higher in the water column, have access to more seston while being less dependent on optimal tripton advection and less at risk of being buried (van der Schatte Olivier et al., 2021).
- While individual larger bivalves with greater tissue content hold a greater quantity of nitrogen and phosphorus compared to smaller bivalves, nitrogen and phosphorus content is comparatively higher in the tissues of smaller bivalves as relative tissue content is greater in rapidly growing juveniles (Smaal & Vonck, 1997).
- A study in Poole Harbour demonstrated that despite individual oysters having a notably larger filtration rate than mussels, especially during the summer season (0.65 - 6.48 L h^{-1} g of oyster dry $weight^{-1}$, 0.90 – 3.30 L h^{-1} g of mussel dry weight), mussels show a higher filtration rate per gram of dry weight (7.5 L h^{-1} g of dry meat weight at 10-15^oC for mussel; 3 - 6 L h^{-1} g of dry meat weight at 15 - 19^oC for oysters) (Gravestock et al., 2020).

1.5. Shell-specific nutrient removal

- Whilst the largest fraction of absorbed nitrogen goes to tissue growth, a smaller fraction of nitrogen is utilised for shell growth (Petersen et al., 2014). Nitrogen indirectly impacts bivalve shell formation by influencing the activity of shell matrix proteins and ion transport mechanisms during the biomineralisation process (Yarra et al., 2021).
- There is a growing interest in the use of oyster shell byproducts for phosphorus absorption as oyster shells absorb a greater ratio of phosphorus than tissue and have been shown to have a higher absorption capacity than many commercial alternatives (Wang et al., 2013).
- In Poole Harbour, bivalve shells and other harvested material are redispersed back to the seabed after harvesting, providing solid sediment for colonising organisms such as bivalves to attach to (Blake & zu Ermgassen, 2015), but limiting the commercial uses of bivalve shells (Summa et al., 2022).
- However, these shells can be buried, essentially removing the nitrogen, phosphorus and carbon from the nutrient cycle for a time. Buried *O. edulis* shells have been estimated to remove an average of 2.1 g of nitrogen m^{-2} yr^{-1} and 2.3 g of phosphorus m^{-2} yr^{-1} from biotopes present across the Solent (Fodrie et al., 2017; Kellogg et al., 2014; Newell et al., 2005; Watson et al., 2020). This represented a greater amount of nitrogen (0.18 g m^{-2} yr^{-1}) and phosphorus (0.1 g m^{-2} yr^{-1}) than is removed through shell growth (Higgins et al., 2011; Watson et al., 2020).

1.6. Biodeposition and Denitrification

- A study by Rice (2001) found that while commercially harvesting shellfish reliably captures nitrogen and phosphorus, the majority of nitrogen and phosphorus capture likely takes place through a combination of sediment burial and denitrification.
- Bivalves transport filtered particles from the water column to the sediment through biodeposition made up of faeces, pseudofaeces, and ammonia. This nutrient exchange between the pelagic and benthic environments contributes to nutrient cycling and boosts bacterial denitrification. This process leads to the removal of nitrogen from the marine ecosystem, helping to alleviate eutrophication (Williams et al., 2018).
- Denitrification is a suboxic process that occurs when organic nitrogen is broken down to inert nitrogen gas and is influenced by numerous water quality parameters in addition to chlorophyll *a* concentration (Kellogg et al., 2014). The process can be separated into two key steps:
    - Nitrification, when ammonium is oxidised to nitrate by nitrifying bacteria in the oxic (oxygen-rich) upper layer of sediments.
    - Denitrification, when nitrate is then reduced to inert nitrogen gas (N_2) by denitrifying bacteria in the anoxic (oxygen-poor) layer of sediments, leading to the removal of nitrogen from the marine system into the atmosphere.
- Nitrification and denitrification rates are species-specific, as highlighted by Petersen et al. (2019) who compiled and compared various bivalve mariculture and reef denitrification rates across literature. Kellogg et al. (2014) points out that denitrification in oyster aquaculture varies significantly in the literature, and is highly dependent on several environmental, seasonal, site-specific and culturing practices.
- Organically enriched sediments can act as either sinks or sources of nitrogen. Enhanced denitrification in these sediments can remove nitrogen from the marine area through the production of nitrogen gas (N_2; nitrogen sink). On the other hand, enhanced dissimilatory nitrate reduction to ammonium (DNRA) and ammonium (NH_4^+) production can increase nitrogen availability in the water column through nitrification (nitrogen source).

1.7. Cultured vs reef bivalve denitrification

- Sediment denitrification rates under oyster reefs more consistently make these habitats net nutrient sinks (Petersen et al. 2019). A study by Watson et al. (2020) shows how Native oyster

(*Ostrea edulis*) reefs in the Solent were estimated to have provided an annual bioextractive value of £37,440,000 for nitrogen and £6,770,000 for phosphorus through a combination of shell nutrient assimilation, burial, and denitrification.

- A study by Kellogg et al. (2013) estimated that annual denitrification rates in restored oyster reefs in the Choptank River, Chesapeake Bay, USA, resulted in the removal of approximately 0.5 tons of nitrogen per hectare per year more than in control plots. However, Kellogg's estimates are unusually high compared to other literature findings (Petersen et al., 2019).
- While wild oyster reefs reliably enhance denitrification rates, sediment denitrification rates under aquaculture beds show significant variation, with some studies recording nitrification outpacing denitrification (Petersen et al., 2019).
- This variability is mainly attributed to the higher quantity of biodeposition from intensive aquaculture. While moderate levels can enhance denitrification, excessive biodeposition can lead to sediment anoxia, which reduces denitrification efficiency (Higgins et al., 2013; Kellogg et al., 2014; Smyth et al., 2016; Lunstrum et al., 2018).
- Areas with low-flow or limited water exchange are particularly prone to sediment anoxia given sufficiently high bivalve densities as limited horizontal transportation can allow for the rapid concentration of biodeposition under bivalve beds (Smyth et al., 2018).
- Temperature, oxygen levels, and nutrient concentrations in the water column impact denitrification processes, resulting in strong seasonal differences, particularly with aquaculture bivalves (Levington & Doall, 2019).
- For example, a study by Humphries et al. (2016) found that denitrification under oyster reefs was greatest during fall when high food availability increased biodeposition.
- However, multiple studies have recorded lower denitrification rates under bivalve farms during the summer. A combination of excessive biodeposition and higher respiration rates from increased temperature and food availability can increase sediment oxygen consumption, thereby creating anoxic conditions that reduce denitrification efficiency (Crawshaw et al., 2019; Murphy et al., 2016).
- Earlier studies in the Wadden Sea and New England, USA, found that sediment denitrification was greatest during winter, suggesting that high nitrogen input, and therefore plankton abundance, can enhance denitrification regardless of temperature (Heiss et al., 2012; Kieskamp et al., 1991).
- Despite the variability in aquaculture denitrification rates compared to established reefs in literature, Petersen et al. (2019) points out that more recent studies have demonstrated comparable denitrification rates in both restored reefs and oyster aquaculture beds (Humphries et al., 2016). This is partially attributed to a study by Caffrey et al. (2016) that found that while both nitrification and denitrification occurred on dead oyster shells, denitrification was greater on living oysters, suggesting that denitrification is enhanced on the surface of living oysters in addition to sediment deposition.
- This additional enhancement of denitrification rates more so benefits managed aquaculture beds that generally have a higher ratio of living to dead shells through operational maintenance, whereas the ratio of living to dead shells in wild biogenic reefs vary significantly (Nestlerode et al., 2017; Salewski, 2021).

1.8. Culture method on denitrification rates

- Lindhal et al. (2005) recorded that a sample of longline 106 *M. edulis* could remove 250 kg of nitrogen when taking into account denitrification from a Swedish fjord, reducing the net transport of nitrogen by 20% over 10 months through benthic-pelagic coupling. Moreover, a study by Labrie et al. (2023) recorded repeated enhancement of denitrification in floating oyster farms between an average of 265-388% above control site levels over the course of 3 years.
- However, denitrification rates on oyster farms were observed to be an order of magnitude higher on bottom cultures in comparison to suspended cultures, with on-bottom cultch oyster cultures producing similar denitrification rates to those observed under restored oyster reefs

(Higgins et al., 2013; Kellog et al., 2014; Sisson et al., 2011). This likely occurred due to the higher rates of biodeposition from faeces and pseudofaeces deposited directly onto the sediment in bottom cultures as opposed to suspended cultures where biodeposition is more easily dispersed (Lunstrum et al., 2018).

- Holmer et al. (2015) suggest that the most effective nitrogen removal may occur when shellfish are growing rapidly and are harvested quickly, typically after about a year. This is because the rapid growth phase maximises tissue nitrogen uptake. Additionally, properly timed harvesting prevents excessive biodeposition that could otherwise lead to increased nitrification which is more likely in larger shellfish that individually produce more biodeposit.
- A study by Humphries et al. (2016) suggested that many previous studies measuring denitrification rate under oyster farms, particularly those that indicated that shellfish aquaculture were carbon sources, did not account for seasonality. Instead, Humphries et al. (2016) reached a similar conclusion to another study observing oysters cultivated on cultch (as is done in Poole Harbour) in Louisiana USA that recorded similar denitrification rates to restored oyster reefs (Sisson et al., 2011).
- An estimate of commercial bivalve nutrient remediation across Europe estimated that cultured bivalves removed 3,519 tonnes of nitrogen and 287 tonnes of phosphorus in 2015, valued at $70,459 and $10,286 respectively when considering harvesting and denitrification (van der Schatte et al., 2020). Globally, mussels removed the most nitrogen tonnage per tonne of shellfish in 2015 (6.66×10^{-3}) followed by clams (2.92×10^{-3}) and oysters (2.33×10^{-3}). For phosphorus, mussels again removed the greatest tonnage per tonnage of shellfish (4.92×10^{-4}) followed by oysters (4.53×10^{-4}) and clams (2.90×10^{-4}).

Summary of Section 1. Nutrient Cycling

- Eutrophication, caused by excessive nitrogen and phosphorus from human activities, leads to algal blooms, oxygen depletion, and habitat degradation.
- In **Poole Harbour**, high nitrogen inputs have resulted in the excessive growth of algae mats, reducing biodiversity in the feeding grounds of protected bird populations (Franklin et al., 2020; Thornton et al., 2020). Nitrogen levels are projected to rise due to run-off from historic fertiliser catchments.
- Filter-feeding bivalves, such as mussels, oysters, cockles and clams remove nitrogen and phosphorus from the water by incorporating them into tissue and shells which can be removed through harvest removal), and through biodeposition that promotes burial and denitrification (Dumbauld et al., 2019).

- Shellfish induced nitrogen removal has been valued at **$70.46M** and phosphorus at **$10.29M** across European shellfish production (van der Schatte Olivier, 2020).
- In Poole Harbour, mussel and oyster farms have been estimated to filter up to 62% of the Harbour on a neap tide (Gravestock et al., 2020). Harvest-based removal estimates have shown that mussels remove **~0.88% of live weight in nitrogen**; oysters remove **0.37%** (Cubillo et al., 2023).
- A proximate analysis of mussel production showed that mussels remove **125–248 tonnes of nitrogen annually** across the UK (GAIN Project, 2018).
- In 2019, total bivalve removal in the UK was estimated at **126–362 tonnes** using a FARM model. Combining these results with local wastewater treatment cost savings, the nitrogen cycling of mussels farmed in Poole Harbour has been valued at **£7M–£21M per year** (Woźniacka, 2024).

- The value of nitrogen and phosphorus removal through shellfish harvesting is gaining traction globally.
  - In Chesapeake Bay, USA, 7.7M oysters removed 1 tonne of nitrogen via growth (Rose et al., 2015).
  - In Japan, Oysters remove ~10% of daily nitrogen load into Hiroshima Bay.
  - In Jiaozhou Bay, China, Manila clams remove 28.7% daily nitrogen loadings and 43.3% daily phosphorus loadings (Zan et al., 2014).
  - UK and EU-Wide estimates valued Shellfish-based mitigation at €11–17 billion annually (Ferreira et al., 2009).

- A study by Rice (2001) suggests that although a significant amount of nitrogen and phosphorus can be removed through harvesting, the majority of nitrogen and phosphorus capture likely takes place through a combination of sediment burial and denitrification.
- Native oyster reefs in the Solent were estimated to have provided an annual bioextractive value of £37,440,000 for nitrogen and £6,770,000 for phosphorus through a combination of shell nutrient assimilation, burial, and denitrification (Watson et al., 2020).
- Generally, Suspended mussel culture remove more phosphorus and nitrogen through harvesting than bottom cultures as suspended bivalves invest in greater tissue growth at the expense of shell growth (van der Schatte Olivier et al., 2021).
- In turn, Bottom cultures can show higher sediment denitrification rates than suspended cultures due to the higher rates of biodeposition from faeces and pseudofaeces that are deposited directly onto the sediment in bottom cultures when compared to suspended cultures (Lunstrum et al., 2018).

- Denitrification rates fluctuate seasonally, with denitrification usually lower in the summer due to higher bivalve respiration rates combined with excessive biodeposition creating anoxic sediment conditions that inhibit the denitrification process (Crawshaw et al., 2019; Murphy et al., 2016).
- While denitrification rates under aquaculture farms are highly variable across literature, recent studies have demonstrated comparable denitrification rates between restored biogenic oyster reefs and oyster aquaculture beds (Humphries et al., 2016; Petersen et al., 2019). This is primarily due to living oyster shells showing higher denitrification rates compared to the dead oyster shells reefs are primarily made of (Caffrey et al. 2016).
- Farmed bivalves across Europe have been estimates to removed 3,519 tonnes of nitrogen and 287 tonnes of phosphorus in 2015, valued at $70,459 and $10,286 respectively (van der Schatte et al., 2020).
- Nutrient cycling is species dependant. In 2015, mussels were shown to remove the most nitrogen tonnage per tonne of shellfish globally (6.66×10^{-3}) followed by clams (2.92×10^{-3}) and oysters (2.33×10^{-3}). For phosphorus, mussels again removed the greatest tonnage per tonnage of shellfish (4.92×10^{-4}) followed by oysters (4.53×10^{-4}) and clams (2.90×10^{-4}) (van der Schatte et al., 2020).

2. Blue Carbon

- Climate change is a growing concern globally, with the UK government aiming to cut carbon emissions by 81% by 2035, to reach net zero by 2050, updating the previous legal requirement to reduce carbon emissions by 78% by 2035 (BEIS 2021; ESNZ 2024)
- Blue carbon refers to carbon that is stored in coastal and marine systems including seagrass beds, salt marshes, and mangroves. These habitats are vital for mitigating climate change, with UK estimates suggesting that they store between 0.2 (119,759 hectares) – 994.9 (5,398,081 hectares) Tg of carbon (Atwood et al., 2020; Macreadie et al., 2021). This highlights the importance of oceans and coastal areas in the biogeochemical cycle of carbon.
- Bivalves, as filter-feeding organisms, take up organic and inorganic nutrients from the water column including dissolved CO_2. Shellfish in particular are of interest as their shells are primarily made from carbon rich calcium carbonate ($CaCO_3$) and can serve as carbon sinks with a relatively long turnover rate, effectively storing carbon.
- Compared to proposed alternative carbon capture forms, shellfish farming has relatively low energy input, low costs, and low technological feasibility (Feng et al., 2023), while offering a wide range of other services and benefits.
- Estimating the carbon sequestration potential of bivalves is difficult due to the number of positive and negative feedback loops involved, ranging from stochiometric to ecosystem-level interactions. Jansen and van den Bogaart (2020) describe 4 different methods of calculating carbon sequestration. In these calculations, shell growth, tissue growth, and sedimentation from biodepositions act as potential sources of carbon sequestration. These processes are then balanced against CO_2 release from respiration, bio-calcification, and remineralisation from biodeposition.

2.1. Shell carbon sequestration

- A study by Tang et al. (2011) suggests that shellfish aquaculture could be a net carbon sink through the sequestration of dissolved inorganic carbon into calcium carbonate through calcification into shell growth, and that it does so far more effectively than terrestrial ecosystems as shells do not degrade as quickly.
- Other studies on *M. edulis* farming have highlighted how shell growth can act as a slight carbon sink when taking into account transport (Aubin et al., 2018; Fry 2012).
- The extent to which calcification can be used to store carbon is ongoing in the literature and varies between species and environmental conditions.
- Bicarbonate (HCO_3^-) is released as a byproduct of shell calcification, resulting in the release of CO_2 (Morris & Humphreys, 2019). The equilibrium of the carbonate system, and therefore the release of atmospheric CO_2, is influenced by many environmental factors such as water pH, temperature, and salinity (Seibel & Walsh 2001; Sunda & Cai 2012).
- A study by Martini et al. (2022) found that *M. edulis* aquaculture in Italy sequestered 0.19 - 0.2 kg CO_2 kg^{-1} per mussel through calcification, whilst releasing only 0.12 kg CO_2 kg^{-1} per mussel, resulting in a net sequestration of 0.07 - 0.08 kg CO_2 kg^{-1} per mussel.
- Higgins et al. (2011) measured that an *M. gigas* farm with a density of 286 oysters m^{-2} sequestered 13.47 ± 1.00 tonnes of Carbon through shell per hectare annually via harvesting.

2.2. Tissue carbon sequestration

- Net tissue growth represents a form of stored organic carbon filtered from the water column whilst respiration releases CO_2 for metabolic processes including shell and tissue growth (Jansen & van den Bogaart, 2020). Up to 90% of stored bivalve energy is allocated to tissue growth and maintenance compared to only 10% for shell growth (Edie et al, 2024).
- Álvarez-Salgado et al. (2022) demonstrated that whilst the carbon footprint of mussel shell formation is constant at 365 kg of CO_2 per ton of shell, tissue organic carbon footprint ranged between 92 to 578 kg CO_2 per ton of tissue.

- Although tissue carbon does not have as long-term a storage potential as shell formation, it represents a potentially greater, albeit more variable form of carbon capture. Tissue is also fully removed from the habitat upon harvest, while shells might be returned to the site depending on local regulations and farming practices.

2.3. Impacts of seasonality and species on carbon sequestration

- The carbon sequestration potential of both bivalve shell and soft tissue is species-dependent. Tamburini et al. (2022) found that Manilla clam sequester more carbon in their shell compared to Mediterranean mussels (*Mytilus galloprovincialis*; 0.254 vs 0.146 kg of CO_2 per 1kg of harvested shellfish), whilst mussels sequester relatively more carbon in soft tissue compared to clams (0.152 kg vs 0.115 of CO_2 per 1kg of harvested shellfish).
- Similarly to nitrogen, mussels dominated in terms of the proportion of total carbon removed by shellfish in the UK (83.51%), with Pacific oysters removing nearly five times less (16.32%), due to both current higher UK production numbers and the greater tissue and shell carbon content (Woźniacka, 2024).
- Under certain environmental conditions, shell formation and respiration in mussels and clams have been shown to release more carbon than is being stored through shell formation (Hily et al., 2013; Mistri & Munari, 2012; Munari et al., 2013).
- Bertolini et al. (2021) modelled Manila clam carbon sequestration potential associated with shell and tissue growth in Venice, taking into account respiration and shell calcification. The bioenergetic model showed notable seasonable variations with the clams becoming a source of CO_2 between November-March, during which no growth occurred but respiration did, and a sink between April – October when shell growth occurred. However, when measured across the year, Manilla clams were shown to be overall moderate CO_2 sinks (-3.6 to -24.4 kg CO_2 ton^{-1} of clams).
- In contrast, a model by Hamer and Foekema (2023) estimated that *M. edulis* shell formation could become a carbon source under predicted temperature rises, releasing more CO_2 during the summer when shell calcification and biomineralization are greatest.
- These seasonal variations were attributed to differences in CO_2 release during calcification/shell formation driven by site-specific and seasonal variables such as pH and temperature (Morris & Humphries, 2019).
- While respiration contributes to ocean acidification by shifting the carbonate equilibrium towards greater atmospheric CO_2 release, acidification is balanced by organic nitrogen release in the form of NaOH and shell calcification (Filgueira et al., 2019).
- Seasonality has been shown to have a strong impact on oyster and mussel filtration rates in Poole Harbour, with chlorophyll *a* filtration in mussels and oysters' greatest between May and August (Gravestock et al., 2020), with potential implications for the sequestration of carbon.
- Algae removal from commercial oysters and mussels in Poole Harbour peaked around June-July following higher temperatures and algae concentrations (Gravestock et al., 2020), which could result in greater carbon absorption through shell and tissue growth during this period as seen in other farms that exhibit a greater nutrient cycling rate and growth in the summer months (Jansen et al., 2012).
- In light of the variation in literature for carbon removal rates associated with bivalve shell and tissue harvesting, Jansen and van den Bogaart (2020) highlights how easily environmental factors can influence the carbon mass balance calculations and the important role bivalve biodeposition can play in tipping bivalve carbon mass balance towards further sequestration.

2.4. Biodeposition carbon sequestration

- The transport of organic carbon to the sediment represents a significant pathway for nutrient cycling and can account for a sizable fraction of blue carbon storage. Once faeces and pseudofaeces are expelled, a fraction of the biodeposit is remineralised by microbial activity, returning carbon to the water column by converting organic carbon into dissolved inorganic carbon and other inorganic nutrients. The remaining effluent is buried, effectively storing carbon in the sediment (Jansen, 2012; Yang et al., 2021).

- Temperature, salinity, growth, algae concentration, and bivalve weight have all been shown to impact organic carbon deposition (Filgueira et al., 2019; Lee et al., 2020).
- Sediments under mussel, clam, and oyster farms show significantly higher organic matter content than control sites (Christensen et al., 2003; Giles et al., 2006; Kim et al., 2020; Mitchell, 2006). However, organic enrichment and carbon deposition rates are seasonal, with Levington and Doall (2019) recording lower organic enrichment under *M. gigas* beds during the colder winter and early spring periods when growth is arrested. In contrast, remineralisation in *M. gigas* farms has been shown to be greater in the summer, suggesting that carbon burial is more efficient during colder periods (Labrie et al., 2022).
- Hydrodynamics is another major factor influencing sedimentation rates. Remineralisation typically occurs in the water column, therefore water depth, bivalve depth in the water column, and sinking rates can influence sedimentation burial (Findlay & Watling 1997; McKindsey et al., 2011). Strong currents increase horizontal biodeposition advection, breaking up and dispersing faeces and pseudofaeces, thereby increasing surface area and the fraction that is remineralised (Giles et al., 2006; Grant et al., 2005).
- In bay systems, the dynamic environment can result in greater dispersion and resuspension despite the shallow depth, limiting carbon burial (Porter et al., 2018). Resuspension can be negligible in sheltered areas with weak currents (Weise et al., 2009), although wind strength can still noticeably impact sediment resuspension in shallow areas (Tang et al., 2011).
- Callier et al., (2006) recorded biodeposition from a mussel farm in Great Entry Lagoon, Canada, only dispersing between 0 - 24.4 m from the farm. However, it was noted that biodeposit resuspension was seasonally dependent on wind strength.
- The carbon sequestration capacity of shellfish is dependent on multiple ecosystem factors. Algae availability will impact tissue and shell growth, and biodeposition makeup through changes in filtration rates as extremes in algae concentrations can influence valve opening duration and particle retention rates (Riisgård et al., 2011).
- Additionally, environmental factors such as current strength and wind speeds can influence deposition suspension times, impacting remineralisation rates and therefore carbon sequestration. This in turn can help explain some of the seasonal variation observed in carbon sequestration (Bertolini et al., 2021) but not variations between studies that took place in the same seasons.

2.5. Culture method impact on carbon content

- Farming methods and culture location in the water column can notably influence tissue growth and bivalve carbon content distribution, with a 50% difference in carbon sequestration for the same mussel species recorded between Aubin et al. (2018) and Fry (2012) attributed to differences in culture methods and life cycle assessment methodologies.
- Bivalves in Poole Harbour are predominantly on-bottom cultures without any structures on the sediment. The only current exception is mussels where both on-bottom and vertical mussel ropes that are suspended from already existing structures are present in the Harbour.
- Aldritch and Crowley (1986) linked a greater energy investment in tissue growth at the expense of shell growth by subtidal mussels to feeding conditions. Higher invertebrate predation pressure and stronger wave force have also been attributed to the relatively higher shell weight seen in bottom-culture mussels when compared to suspended cultures (Lowen et al., 2013; Steffani & Branch, 2003).
- An analysis of UK farms show that per kg of mussel, tissue carbon content is higher in suspended mussel cultures at the expense of shell carbon, whilst the inverse is true for bottom cultures (Jansen & van den Bogaart, 2020).
- On-bottom mussel cultures have greater shell carbon sequestration potential when compared to suspended mussel rope cultures which may be more suitable for food production given their higher flesh-to-shell ratio. This translates to significantly more carbon sequestered into long-

term shell storage in bottom mussel cultures (60.15 ± 0.77 kg) compared to rope cultures (46.12 ± 1.69 kg) observed across multiple UK sites (van der Schatte Olivier et al., 2021).

- On-bottom bivalve cultures expel faeces and pseudofaeces directly into the sediment, enhancing the burial of organic material into the sediment. In contrast, suspended cultures are more likely to have their biodeposition dispersed, increasing the rate of remineralisation before sedimentation can occur (Gu et al., 2022).
- Smaller bivalves of the same weight as larger individuals (higher tissue to shell ratio individuals) demonstrate higher clearance rates, but lower carbon deposition rates per unit weight (Ahn 1993; Tsuchiya, 1980). This could reflect a potential trade-off between optimum nitrogen and phosphorus sequestration, and optimum carbon sequestration as a significant majority of absorbed nitrogen and phosphorus is utilised for tissue growth (Edie et al, 2024).
- However, bivalves with a higher tissue to shell ratio are likely to have higher metabolic rates and therefore higher biodeposition rates (Mesnage et al., 2007). Depending on bivalve density and environmental conditions, rapid biodeposition build-up can decrease sediment denitrification by promoting anoxic conditions as recorded in multiple shellfish farms (Burkholder & Shumway 2011; Cranford et al., 2002; Murphy et al., 2019)
- The complexity of bivalve nutrient cycling and the difficulty in optimising the value of bivalve ecosystem services highlights the importance of best management and cultivation practices.
- Literature comparisons of the impact of different cultivation methods on carbon sequestration vary as a result of numerous environmental conditions and subsequent feedback loops, but when accounting for all carbon sequestration pathways, an analysis of multiple mussel farms suggests that carbon sequestration is relatively similar between bottom and suspended mussel cultures, with a slight trend towards bottom cultures (Jansen & van den Bogaart, 2020).

2.6. Dredging impact on carbon sequestration

- Dredging is by far the most dominant bivalve harvesting method in Poole Harbour. The impact of dredging on sediment organic matter and blue carbon stores is complex and driven by various biotic and abiotic factors (Epstein et al., 2022).
- Demersal fishing activity in general can result in the temporary resuspension of large volumes of sediment and therefore stored carbon, enhancing remineralisation (Luisetti et al., 2019).
- Dredging can remove bioturbators that enhance carbon sequestration by facilitating organic matter transportation to deeper sediment. The resistance of bioturbating organisms to dredging is highly site-specific, gear-dependent, and species-dependent (De Borger et al., 2020).
- A study by Clarke et al. (2018) did not show that pump-scoop dredging used in Poole Harbour had altered the organic matter content of non-intensively dredged sites despite observing a loss of fine sediment. Whether the loss of fine sediment encourages remineralisation, decreasing carbon storage, or if the sediment is reburied nearby, is heavily site-specific and dependant on the fishing method (Epstein et al., 2022).
- Despite the lack of data on Poole Harbour sediment carbon content, an estimated ~0.002 Gt of organic carbon is remineralised from UK shelf sediments annually (Luisetti et al., 2019).

2.7. Indirect carbon sequestration

- Regardless of the carbon sequestration calculation used, available literature leans towards shellfish aquaculture being a carbon sink, or at least carbon neutral (The Aquaculture Advisory Council, 2022), in addition to the other services offered by wild and cultured bivalves.
- When using the life cycle assessment method that includes the CO_2 output of the entire production chain (transport, packaging, materials etc.), both *M. galloprovincialis* and *R. phillipinarum* aquaculture offset a significant amount of carbon, with a net CO_2 balance of -91 and -233g CO_2 per 1kg of mussels and clams harvested respectively (Tamburini et al., 2022).
- In light of the variability in the value of bivalve aquaculture as blue carbon storage, Filgueira et al. (2019) emphasised the additional ecosystem services provided by bivalves that impact carbon and nutrient cycling, which is further discussed in the Natural Capital section of this review.

Summary of Section 2. Blue Carbon

- Blue carbon refers to carbon stored in coastal and marine ecosystems including seagrass beds, salt marshes and mangroves. UK coastal habitats store between 0.2 – 994.9 Tg of carbon (Atwood et al., 2020).
- Bivalves have the capacity to act as carbon sinks by absorbing dissolved CO_2 from the water column and forming calcium carbonate ($CaCO_3$) shells. Additionally, shellfish farming has low energy input, costs, and tech requirements compared to other carbon capture methods (Feng et al., 2023).
- Estimating bivalve carbon sequestration is complex due to the number of positive/negative feedback loops. Shell growth, tissue growth, and sedimentation from biodepositions act as potential sources of carbon sequestration. In contrast, respiration, bio-calcification, and remineralisation from biodeposition processes release CO_2. (Jansen & van den Bogaart, 2020).

- Bivalve growth has been shown vary between being a net carbon source and sink across multiple studies depending on various environmental factors including water temperature, pH and salinity (Jansen & van den Bogaart, 2020; Morris & Humphreys, 2019).
- Shells represent carbon storage with a slower degradation rate than other terrestrial carbon sinks (Tang et al., 2011) however, calcification has been recorded as both a carbon source and sink in literature, varying between species and environmental conditions.
- Martini et al. (2022) took into account CO_2 release from bicarbonate production during shell production in an Italian *M. edulis* farm and found that shell production was an overall moderate net carbon sink (0.07 - 0.08 kg CO_2 kg^{-1} per mussel).
- Meanwhile 90% of bivalve energy is allocated to tissue growth vs. only 10% to shell growth (Edie et al., 2024). While the carbon footprint of shell formation is 365 kg CO_2 per ton, tissue carbon capture can vary between 92–578 kg CO_2 per ton (Álvarez-Salgado et al., 2022).
- Tissue is also fully removed from the habitat upon harvest, while shells might be returned to the site depending on local regulations and farming practices. Oyster farms have also been shown to sequester 13.47 ± 1.00 t C ha^{-1} yr^{-1} at high stocking densities through harvesting (Higgins et al., 2011).

- Carbon sequestration varies by species. Manila clams store more carbon in shells whilst mussels store more in soft tissue (Tamburini et al., 2022). In the UK, mussels account for the majority of bivalve carbon sequestration (~83.51% of total carbon), followed by Pacific oysters (~16.32%), primarily due to the greater tissue and shell carbon content and current UK production levels (Woźniacka, 2024).
- Models also show that bivalves carbon sequestration is highly seasonal (Hily et al., 2013). Manila clams can become CO_2 sources in winter (due to respiration without growth) and sinks in summer due through shell and tissue growth (Bertolini et al., 2021).
- Mussel shell calcification may become a net carbon source under rising temperatures, with implications for climate change (Hamer & Foekema, 2023).
- Despite the lack of literature for blue carbon stocks in Poole Harbour, mussel and oyster filtration rates peak in May–August, affecting nutrient cycling and carbon capture (Gravestock et al., 2020).
- Sediment carbon storage is also seasonal as Levington and Doall (2019) recorded lower organic enrichment under *M. gigas* beds during the colder winter and early spring periods when growth is arrested.
- In contrast, remineralisation in *M. gigas* farms has been shown to be greater in the summer, suggesting that carbon burial may be efficient during colder periods (Labrie et al., 2022).
- Water depth, hydrodynamics and wind speed have been shown to impact carbon storage by increasing remineralisation rates (Bertolini et al., 2021; Findlay & Watling 1997; McKindsey et al., 2011; Tang et al., 2011)
- Culture method can notably influence carbon sequestration, tissue growth, and biodeposition. Bottom bivalve cultures have been shown to sequester more carbon than suspended cultures primarily due to lower remineralisation rates (Gu et al., 2022).
- The extent to which dredging limits carbon sequestration potential in Poole Harbour through resuspending buried carbon is multi-faceted and requires further research.
- When using the life cycle assessment method, both *M. galloprovincialis* and *R. phillipinarum* aquaculture offset a significant amount of carbon, with a net CO_2 balance of -91 and -233g CO_2 per 1kg of mussels and clams harvested respectively (Tamburini et al., 2022).

3. Natural Capital – Ecosystem Impacts

- Ecosystem services are reliant on varying forms of capital assets such as social capital which includes institutions, and human capital such as knowledge and skills (Guerry et al., 2015). Natural capital refers to ecosystem-based capital including the shellfish stocks themselves, as well as the habitats and the wider ecosystems that support them (Emery & Flora, 2020).
- Shellfish provide numerous services in addition to being an important food source. Through their positive impact on water quality and maintenance, they support surrounding habitats such as seagrasses, wetlands and mud flats and indirectly enhance the ecosystem services provided by those habitats and the species that depend on them.

3.1. Seagrass and saltmarsh enhancement

- Shellfish filter seston, inorganic particles, and organic detritus reducing water turbidity and increasing light penetration. Increased light penetration and nutrient deposition can enhance photosynthesis at greater depths thereby benefiting benthic primary producers such as seagrass and macroalgae. (Carroll et al., 2008; Newel & Koch, 2004).
- Additionally, while nitrogen is usually the more limiting nutrient when it comes to coastal eutrophication, Shih and Chang (2015) point out that the capacity of bivalves to store phosphorous has been suggested to help regulate phosphorous build-up in nearby wetlands, combating shoreline eutrophication in addition to providing other ecological benefits (Green et al., 2018).
- Seagrass beds and saltmarshes are unique, protected habitats (European Commission, 1992; OSPAR, 2008) that themselves are rich in biodiversity for both terrestrial and aquatic organisms. They provide a variety of ecosystem services including acting as nurseries, refuges, and feeding grounds for many protected and commercially important species (Bertelli and Unsworth, 2014; Green et al., 2009).
- Seagrass beds also show vulnerability, with the UK having lost an estimated 41% of its seagrass beds since 1936 (Green, 2020). Bivalve filtering can sequester nitrogen from terrestrial run-off, which has been identified as the causative factor of the expansion of green *Ulva lactuca* algae beds in Poole Harbour. This species form beds that produce toxins that inhibit seagrass growth and reduce the abundance and diversity of invertebrates in mudflats that act as important feeding grounds for birds (Thornton et al., 2020). Slowing the growth of *U. lactuca* beds via bivalve nitrogen sequestration could increase biodiversity across Poole Harbour, and the resilience of biologically rich ecosystems including mudflats and seagrasses (MacKenzie, 2005).
- Natural England (2018) highlight the negative impact of moderate epiphyte loads and wasting disease coverage on seagrass beds in Poole Harbour. Bivalve filtration has been attributed to a reduction in epiphytes on temperate seagrass beds near aquaculture sites by filtering seston and rapidly recycling nitrogen from the water column (Howarth et al., 2022).
- Seagrass rhizomes stabilise sediment, further decreasing water turbidity, and enhancing nutrient cycling through burial and denitrification, thereby combating eutrophication (Eyre et al., 2011). *Zostera marina* beds in Poole Harbour are a significant carbon sink in the context of European climate change goals, with *Z. marina* having been recorded to store a median of 110 g Carbon m^{-2} yr^{-1} through burial (Burrows et al., 2017).
- Although seagrass beds can be a source of phosphorus depending on environmental factors, *Z. Marina* has been shown to store a median of 18.2 g of nitrogen m^{-2} y^{-2} through burial and denitrification processes (Burrows et al., 2017; Eyre et al., 2016). This is more so the case with coastal salt marshes which have higher reported Nitrogen, Phosphorus and Carbon storage potential per m^{-2} than either seagrass beds or oyster reefs (Watson et al., 2020).
- In addition to nutrient cycling, seagrass beds and salt marshes reduce coastal erosion and can dissipate kinetic wave energy with sufficient coverage, providing additional value as coastal defence and support for other vegetative habitats (Fonseca & Cahalan, 1992; Gracia et al 2018; Möller et al., 2014; Plumlee et al., 2020).

- Whilst shading, ammonium excretion (Vinther & Holmer, 2008), and sedimentation from shellfish farms can negatively impact seagrass beds, these impacts appear to have a much shorter effective distance than the benefits derived from improved water quality (Ferriss et al., 2019; Howarth et al., 2022). These findings suggest that bivalve aquaculture can enhance carbon sequestration and nitrogen cycling in seagrass beds if appropriate distances are maintained between farms and carbon sink ecosystems.
- Likewise, bivalve aquaculture can support saltmarshes through the same processes as biogenic reefs, increasing sediment stability and combating eutrophication (Castagno, 2018).

3.2. Plankton cycling

- The impact of shellfish on phytoplankton production is complex. Various feedback loops between nutrient cycling and water quality can alter seston assemblages. Any changes to the make-up of marine seston is likely to have a notable impact on nutrient cycling and the wider marine ecosystem given the role of phytoplankton as primary producers.
- Although high densities of bivalves can reduce primary production and therefore CO_2 absorption (Smaal & Prins, 1993), low densities of *Mercenaria mercenaria* have been shown to double primary production in nutrient-poor conditions (Doering et al., 1987). A study by Giles et al. (2006) showed that 94% of primary production nitrogen requirements in a site in New Zealand was released by farmed mussels. The frequent filtering of seston coupled with ammonium excretion increases nutrient cycling and availability.
- However, shellfish graze selectively and can alter phytoplankton assemblages based on species-specific retention efficiency and nutrient content which can alter local carbon uptake (Filgueira et al., 2019). Prins et al. (1995) provide an example where the presence of *M. edulis* led to a planktonic shift from larger, slower-growing species to more rapid-growing algae species.
- A similar shift away from slower growing species has been observed in Poole Harbour where the composition of phytoplankton has changed from diatom species characteristic of low nutrient conditions in 1980s replaced by those typical of lower nutrient conditions. Crossley (2019) attributed this planktonic shift to increased nutrient run-off from post World War 2 agricultural practices and increased sediment accumulation.
- Higher planktonic growth rates increase CO_2 fixation during photosynthesis, thereby transferring carbon from the water column into the biosphere where carbon sequestration is possible (Filgueira et al., 2019). Additionally, increases in nutrient turnover from faster growing phytoplankton such as diatoms have been shown to increase biodeposition, thereby enhancing denitrification (Lucas et al., 2016).
- Some bivalve species including *M. edulis* have shown a preferential uptake for harmful algae bloom (HAB) species (Hegaret et al., 2007), suggesting that bivalve aquaculture has the potential to contribute to HAB management and public safety.
- Findings from a study in China, found that Chinese pleated oyster (*Crassostrea plicatula*) reduced phytoplankton abundance by 46.3% whilst increasing seston species richness by 26.3 – 38.3% in an environment suffering from anthropogenic sourced eutrophication (Jiang et al., 2019).
- A study investigating the environmental impact of *R. philippinarum* farming in China found that models suggested that *R. philippinarum* presence disturbed existing macrofauna through seston depletion and increased biodeposition. This coincided with a greater macrofaunal species richness and abundance attributed to greater carbon flux (Sun et al., 2023).
- A study by Rahman et al. (2020) demonstrated that the retention efficiencies of mussels (*Mytilus galloprovincialis*), oysters (*M. gigas*), and cockles (*Katelysia rhytiphora*) change seasonally, effectively filtering seston ranging from bacteria and detritus to mesozooplankton (Lehane & Davenport, 2002; Davenport et al., 2011), thereby reducing food competition between bivalves.

3.3. Biogenic reef enhancement

- Clams and cockles modify their habitats through filtration, bio-deposition, and settlement. However, mussels, and to a greater extent oysters, are unique as they display aggregating behaviour, forming comparatively more extensive, structurally complex biogenic reefs (Christensen et al., 2015; Rodriguez-Perez et al., 2019).
- Biogenic reefs provide many of the same ecosystem services as aquaculture. Studies on nutrient cycling in biogenic reefs have consistently recorded enhanced denitrification rates and considerable carbon storage (Jansen & van den Bogaart, 2020; Petersen et al., 2019).
- Various studies have highlighted the increase in flora and fauna biodiversity and eutrophication mitigation value of *M. edulis* reefs (Norling & Kautsky, 2007; Petersen et al., 2016; Stounberg et al., 2024).
- A study investigating Chichester Harbour found that *O. edulis* biogenic reefs have declined by 96% over 19 years (Helmer et al., 2019). The decline of *M. edulis* reefs in Denmark has been associated with deteriorating water quality and biodiversity loss, with reports of mussel populations across the Swedish coast suggesting that *M. edulis* has disappeared from the West coast (Baden et al., 2021; Kristensen et al., 2015).
- As with other ecosystems discussed above, these wild populations benefit from the increased water quality associated with eutrophication mitigation and can in turn contribute to the removal and storage of nitrogen, phosphorus and carbon (Bishop et al., 2023).
- Wild biogenic reef development alters sediment makeup and complexity, often stabilising sediments and enhancing invertebrate biodiversity, thereby increasing fish abundance (La Peyre et al., 2014).
- A growth model by Peterson et al. (2003) suggested that restoring historic oyster reefs in Louisiana USA could increase the catch of commercially valuable finfish and crustaceans by 2,600 kg ha^{-1} yr^{-1}. A follow-up study found that the value the restored reefs provide through fisheries enhancement was greater than the commercial value of the oysters themselves, with the oyster reef adding $3,811 ha^{-1} yr^{-1} of value to local fisheries (Grabowski & Peterson, 2007). Additionally, an estimated added value of $3,000,000 to sports fishing in Louisiana was directly attributed to increased sporting interest following higher finfish abundance and diversity supported by the restored reefs (Isaacs et al., 2004).
- Redepositing shells on the seabed, as is done in Poole Harbour, provides solid settlement material for wild and cultured spat to attach to. For example, multiple bivalve species have been shown to settle on oyster shells. Fey et al. (2010) points out that mussel populations in the Wadden Sea were enhanced by the presence of oysters despite food and space competition. This was attributed to access to solid settlement as settling material is often a limitation for bivalve recruitment.
- A lack of solid sediment is one of the major obstacles associated with *O. edulis* reef restoration efforts (Goelz et al., 2020; Housego & Rosman 2016). By returning shell and other solid sediment to the seabed, aquaculture operations in Poole Harbour may offer some of the same benefits as provided by biogenic reefs.
- Biogenic reefs are unlikely to re-establish themselves in Poole Harbour to historic levels as it is a spatially competitive area with ongoing channel dredging to allow for vessel traffic. Comparative studies on the development of wild *M. gigas* reefs in Poole Harbour and Southampton Waters show that *M. gigas* recruitment is highly variable in Poole Harbour with significantly lower abundances than in Southampton Waters despite ongoing (triploid) *M. gigas* aquaculture operations in Poole Harbour (Mills, 2016; Noble, 2022; Phillips, 2022).
- The variable *M. gigas* abundances observed in Poole Harbour compared to the formation of colonies observed in Southampton Waters have been attributed to a range of factors, including greater exposure to strong southernly winds and tidal forces, and anthropogenic disturbances (Mills, 2016).
- While deposited shells enhance bivalve recruitment, these shellfish are ultimately harvested by dredging and removed from the system, stifling reef establishment. However, diploid cultured bivalves can act as spat sources that enhance the recruitment of wild bivalve populations (Bishop et al., 2023; Norrie et al., 2020).

- In addition to nutrient cycling and enhancing nearby ecosystems, biogenic reefs alter the benthic habitat from sand-dominated habitats to boulder reefs, increasing the structural complexity of the sediment and exerting a strong influence on local hydro-dynamics (Lovelock & Duarte, 2019). These reefs can impact hydrodynamics by dissipating wave energy, and therefore affect ecological processes hundreds of meters from the reefs (Fivash et al., 2021; Ysebaert et al., 2019) helping to reduce coastal erosion.
- As a result, there is growing interest in the value of biogenic reefs for coastal protection as oyster reefs can serve as living, expanding breakwaters that reduce coastal erosion whilst increasing biodiversity (Scyphers et al., 2015).
- The impact of bivalve aquaculture on wild populations is heavily site specific and is dependant on the major limiting factors affecting bivalve growth (Gallardi, 2014). Cultured and wild bivalves compete for phytoplankton, therefore under oligotrophic conditions when food availability is limited food competition can negatively impact wild populations, particularly as cultured bivalves typically have a faster growth rate (Capelle et al., 2017; Ferreira et al., 2018).
- However in nutrient-rich systems such as Poole Harbour (Crossley 2019), poor water quality and lack of solid sediment is likely to be a greater limiting factor to wild bivalve growth (Cranford et al., 2003; Gravestock et al., 2020).
- Additionally, despite aquaculture movement being a significant vector for bivalve disease transmission (Brenner et al., 2014), greater denitrification rates may remove pollutants from the water column and reduce the transmission of disease to bivalves and other organisms through filtration and burial (Broszeit et al., 2016; Burge et al., 2016).
- Thieltges et al. (2009) found that the presence of *M. gigas* in the List tidal basin, Germany, coincided with reduced parasite loads and infections in *M. edulis.* Eutrophication mitigation and solid sediment provided by bottom-cultured bivalves could therefore enhance wild beds despite greater competition (Bishop et al., 2023; Gallardi, 2014).

Summary of Section 3. Natural Capital

- Shellfish contribute to ecosystem health beyond food production by improving water quality and supporting habitats like seagrasses, wetlands, and mudflats (Emery & Flora, 2020).
- Seagrass beds and saltmarshes serve as biodiversity hotspots and provide habitat for protected and commercially valuable species (Bertelli and Unsworth, 2014; Green et al., 2009). However, historical losses of UK saltmarsh (38%) and seagrass (41%) in the late 19th century highlights habitat vulnerability (Carroll et al., 2008; Newel & Koch, 2004).
- Eutrophication has been identified as a significant cause of the decline of seagrass beds and saltmarsh coverage in Poole Harbour. Bivalves help regulate nitrogen and phosphorus buildup, aiding in eutrophication mitigation (MacKenzie 2005; Natural England 2018)).
- Shellfish filtration reduces water turbidity, allowing more light penetration, enabling photosynthesis at greater depths which benefits seagrass and macroalgae growth (Carroll et al., 2008; Newel & Koch, 2004).
- Bivalve nitrogen sequestration can reduce harmful algal beds (*Ulva lactuca*), which threaten seagrass and invertebrate biodiversity (Thornton et al., 2020). Additionally, bivalve farms have the capacity to reduce epiphyte coverage on seagrass near aquaculture sites, promoting healthier seagrass ecosystems (Howarth et al., 2022).
- Increasing the resilience of vegetative habitats can reinforce beneficial feedback loops. Seagrass stabilizes sediments, enhances nutrient cycling, and sequesters carbon and nitrogen (Eyre et al., 2011). Saltmarshes can store more nitrogen, phosphorus, and carbon per unit area than seagrass beds or oyster reefs (Burrows et al., 2017; Watson et al., 2020).
- Both seagrass and saltmarshes provide coastal protection by reducing erosion and dissipating wave energy (Gracia et al 2018; Möller et al., 2014; Plumlee et al., 2020).
- Bivalve aquaculture can enhance carbon sequestration and nitrogen cycling in seagrass beds if appropriate distances are maintained between farms and seagrass beds (Ferriss et al., 2019; Howarth et al., 2022).

- Shellfish impact phytoplankton production through feedback loops that alter seston composition. While high bivalve densities may reduce CO_2 absorption (Smaal & Prins, 1993), low densities can enhance primary production (Doering et al., 1987; Giles et al., 2006).
- Bivalves recycle nutrients, supporting phytoplankton growth whilst enhancing denitrification processes (Giles et al., 2006; Lucas et al., 2016). Species-specific filtration preferences can shift plankton assemblages towards more rapidly growing plankton, influencing carbon sequestration (Filgueira et al., 2019).
- Some bivalves including *M. edulis* have been shown to selectively consume harmful algal bloom (HAB) species, helping mitigate HAB risks (Hegaret et al., 2007).
- Bivalve presence can enhance biodiversity by increasing seston species richness and supporting macrofaunal abundance (Sun et al., 2023).
- Seasonal variations in bivalve filtration behaviour reduce food competition and maintain balanced ecosystems (Rahman et al., 2020).

- Mussels and oysters form complex biogenic reefs that enhance biodiversity, increase denitrification rates, and reliably store carbon (Jansen & van den Bogaart, 2020; Petersen et al., 2019).
- Native oyster reefs have declined by 96% in Chichester Harbour over 19 years (Helmer et al., 2019). Similar declines in Denmark were followed by significant water quality deterioration and a loss of biodiversity (Baden et al., 2021; Kristensen et al., 2015).
- Biogenic reefs stabilize sediments, improve invertebrate biodiversity, and boost fish abundance (La Peyre et al., 2014). As a result, restoring oyster reefs can significantly enhance commercial and recreational fishing value and provide greater economic value than the oysters themselves (Grabowski & Peterson, 2007; Isaacs et al., 2004; Peterson et al., 2003).
- Reef restoration in Poole Harbour is unlikely due to high spatial competition and dredging. However, farmed diploid bivalves can act as spat sources that enhance the recruitment of wild bivalve populations (Bishop et al., 2023; Norrie et al., 2020).
- Although aquaculture is a frequent cause of disease transmission (Brenner et al., 2014), bivalve farms have been observed to reduce disease prevalence among marine life including wild bivalves populations by improving water quality (Broszeit et al., 2016; Burge et al., 2016; Thieltges et al., 2009).

4. Food Security

4.1. Food source

- In light of growing global food security concerns and the increasingly limited space for terrestrial meat production expansion, aquaculture is a rapidly growing food sector with global production reaching 130 million tonnes in 2022, surpassing capture fisheries as the biggest aquatic animal producer (Campbell et al., 2017; FAO, 2024). Global bivalve mariculture was recorded at 17.7 million with a global value of $29 billion annually (FAO, 2022).
- Despite this global increase, domestic demand for bivalve consumption has fallen with the UK having a consumption rate per capita of only 0.7 kg compared to Portugal, France and Spain that ranged from 4-8 kg per capita in 2022 (Willer & Aldridge, 2023).
- A survey of UK consumers primarily attributed this decline to bivalve taste, texture and inconvenient preparation (Willer et al., 2021)
- Despite not receiving as much media attention as finfish (Grant & Strand, 2019), bivalve tissue is high in protein, essential fatty acids and an assortment of valuable metabolic minerals (Silva et al., 2021; Venugopal & Gopakumar, 2017; Wright et al., 2018).
- In addition to the value of consuming the whole animal as a food source, there is growing market interest in bivalves as a natural and sustainable source of omega-3 LC PFAs for use as an ingredient for essential oil supplements (Tan et al., 2020).
- Bivalves are unique as one of the few food sources where the entire animal is consumed including the gut (Lee et al., 2008). As a result, any micronutrients consumed by bivalves shortly before consumption will also be digested by humans. A study by Willer and Aldridge (2021) highlights the opportunity presented by the final depuration stage of the shellfish production chain to introduce vital vitamins and micronutrients such as vitamins A and D to increase shellfish value, palatability and combat global vitamin deficiencies (Ritchie and Roser, 2017). Vitamin D deficiency is a growing health problem that disproportionally affects people in lower socio-economic areas, with an estimated 20% of people in the UK exhibiting vitamin D deficiency, (Lin et al., 2021; Sutherland et al., 2021).
- As filter feeders, bivalves occupy a low position in the food chain that does not require additional feed by a farmer. Given that feed costs can make up the majority of finfish aquaculture costs and are associated with declining water quality (Rana et al, 2009; Jiang et al., 2022), low trophic aquaculture, including bivalves and seaweed, represent an opportunity to expand low-cost, highly nutritious protein production while limiting if not mitigating environmental costs (Fry et al., 2018).
- Additionally, bivalve aquaculture does not typically involve the introduction of antibiotics to waterbodies, with disease-resistance steps normally restricted to on-shore hatcheries in controlled/isolated environments (Potts et al., 2021).
- These combination of factors “future proofs” bivalves as a sustainable, highly affordable domestic food source at a time when other major food sectors face sustainability challenges (Grant & Strand, 2019; Kumara et al., 2023).
- As well as human consumption, Bivalve meat can be used to supplement livestock diets including poultry feed, and as a fishmeal replacement for a more sustainable alternative protein source (van der Heide et al., 2021).
- Despite the recognition of the UK shellfish maritime industry as a key sector in sustainable food growth and food security (DEFRA, 2015), UK bivalve production has declined by 62% since its peak in 2008 (Guillen & Virtanen, 2021).
- As a result, there has been a renewed focus in recent years by UK governments to grow the industry, with the English Aquaculture Strategy targeting an UK mussel production increase of 30,000mt by 2040 (Huntington & Cappell, 2020).

4.2. Fisheries

- The value of aquaculture in Poole Harbour was estimated at £2.6 million in 2018 (Williams & Davies, 2018), with the majority of bivalve mariculture production in England consisting of *M. edulis* (67%) and *M. gigas* (32%) (Huntington et al., 2023).
- Aquaculture in Poole Harbour is notable for containing the greatest production of *M. gigas* in England. The UK oyster fishery, which relies on *M. gigas* for over 95% of its landings, was valued at over £13 million in 2012. Landings have since increased from 450 tonnes in 2011 to 1150 tonnes in 2021 (FAO, 2021; Humphreys et al., 2014 & 2021).
- The FAO (2022) recorded 464 companies with 2,833 full-time employees across the UK aquaculture sector in 2018. While employment figures for UK shellfish mariculture are scarce, the industry supports numerous jobs, especially in rural coastal communities where secure employment is scarce, making it a vital source of livelihood (Bonner-Thompson & McDowell, 2020).
- In addition to the value provided by the growth, harvest and sale of cultured bivalves and the jobs provided by the aquaculture industry supply chain, bivalve aquaculture provides added value to numerous other industries through ecosystem services and economic linkages.
- Bivalve aquaculture can enhance wild bivalve fisheries by improving water quality and providing a source of spat (Bishop et al., 2023). Poole Harbour's landings included 583 tonnes in 2017, composed of a variety of commercially important species, notably plaice, sole, bass, Manila clam, common cockles, whelks and brown crabs. These 2017 landings were valued at £1.6 million (Williams & Davies, 2018).
- The abundance and diversity of invertebrates and fish appear to correlate with solid sediment availability and greater habitat complexity. Rapid nutrient cycling organically enriches sediment, supporting herbivorous fauna that in turn attract commercially and ecologically important predators (Newell, 2004).
- The Ropes to Reefs project investigated the impact of mussel longline aquaculture in the Lyme Regis MPA on biodiversity. The project found that the presence of mussel ropes in the previously heavily fished areas introduced solid sediment to homogenous sandy systems, increasing benthic biodiversity by 30% (Mascorda-Cabre et al., 2023).
- Increased habitat complexity and invertebrate diversity enhanced common fishery and angling species over time including mackerel, cuttlefish, and thornback ray (Mascorda-Cabre et al., 2024). The presence of bivalve farms can therefore have a spillover effect in historically fished areas, enhancing the population of commercial species and the fisheries that depend on them as is the case with natural reefs (Mascorda-Cabre et al., 2021).
- As a result, aquaculture gear such as cages and mesh are associated with greater biodiversity (Martínez-Baena et al., 2022). Suspended off-bottom aquaculture techniques show a greater increase in invertebrate and finfish abundance and species richness compared to traditional structureless on-bottom techniques (Munsch et al., 2021; Theuerkauf et al., 2022).
- On-bottom bivalve aquaculture still provides habitat complexity whilst increasing nutrient cycling. Cultured oyster and mussel beds in particular show greater invertebrate and fish biodiversity compared to other commercial bivalves that burrow into the sediment (Theuerkauf et al., 2022). Sustained cultivation of these species introduces heterogeneity to otherwise sandy-sediment systems, increasing infaunal and epifaunal biodiversity and abundance (McKindsey et al., 2007).
- Bivalve aquaculture can improve the resilience of vegetative habitats that act as fish nurseries, especially in areas with high nutrient runoff (See Section 3.1). Bertelli and Unsworth (2014) identified 9 commercially fished species in the UK, including plaice, pollock, and herring, whose population was enhanced by the presence of Zostera marina beds which can be made more resilient by shellfish aquaculture.
- Likewise, a study of intertidal habitats along the Essex coastline found that salt marches also support significant juvenile fish communities including important commercial finfish such as herring and sea bass (Green et al., 2009). The expansion of these stocks can provide other

forms of capital by supporting fisheries, and the communities and industries that depend on them (Herrera et al., 2022).

- Most notably, plaice, sole and bass are culturally and economically significant for Poole Harbour in terms of commercial fishing landing tonnage and recreational angling, particularly Poole's charter boat fleets which has historically strongly relied on bass. The recreational and small-scale commercial fisheries of Poole Harbour represent £9,900,000 of total economic value in 2017 (Williams & Davies, 2018).
- The total value of sea angling in the UK was estimated to be between £1.5 – 2 billion in 2017, directly and indirectly supporting 15,000 jobs (Hyder et al., 2020). In 2018, the charter fleet in Poole had an estimated turnover of £2 million per year, employing 55 people directly in charter boat fishing and an additional 9 in angling shops. Sea angling activities provide additional value to a variety of supporting industries such as hotels and B&Bs, food and drink, fuel and transport businesses (Stebbings et al., 2020; Williams & Davies, 2018).
- An increase in fishing and quayside activities impacts associated economic linkages, providing employment to those involved in vessel sales and maintenance. Additionally, mooring, license, insurance, and parking fees that provide borough councils with additional revenue (Williams & Davies, 2018).
- According to a report by British Marine (2023), the UK marine sector was valued at £17.38 billion, with the direct Gross Value Added contribution of the UK marine industry to the country's Gross Domestic Product was £1.68 billion for the year 2022-2023. This represents a 6.7% increase from the previous year, with a total of 12.5% growth in industry revenue.

4.3. Cultural services

- Cultural services are nebulous and difficult to quantify and are often subjective as the interactions between humans and the natural world changes over time through societal and historical influences (Chan et al., 2012; Jones et al., 2016). As a result, cultural services are the most difficult ecosystem service to quantify however, shellfish aquaculture provides a range of visible cultural services (zu Ermgassen et al., 2020).
- Much of the cultural value of bivalves relates to their historical role as a food source. The harvesting of shellfish for food, has been intertwined with human evolution since before recognisable human civilisations emerged and has been identified as a notable factor influencing early human migrations and settlement (Hausmann et al., 2021; Klein & Bird, 2016).
- Harvested bivalves are consequently important in broad areas of research ranging from anthropological investigations into the societies and movements of early man including diets, tools use and artisanal pursuits (Mannino & Thomas, 2002; Kubicka et al., 2017; Solana et al., 2011; van der Schatte Olivier et al., 2020), to radiocarbon dating studies investigating geochemical changes to marine environments in the distant past to inform on climate change (Butler et al,. 2019; Klishko et al., 2020).
- The prevalence of bivalve harvesting and its formative impact on culture and livelihoods have and continue to contribute to many cultural services ranging from public services and private enterprises, to heritage and spiritual significance. (van der Schatte Olivier et al., 2020).
- Interviews with fishermen show that shellfish fishing is often seen as a way of life rather than a job, with many shellfishers coming from generations of earlier shellfishermen (Holland et al., 2020; Williams & Davies, 2018). These jobs provide spiritual value in addition to supporting connections between identity, place and ownership (Krause et al., 2019; Urquhart & Acott, 2014).
- Interviews with American farmers working in the shellfish aquaculture industry also highlight the additional pride and job satisfaction gained from working in a novel industry, providing avenues of entry into the industry for people who do not necessarily have family traditions of shellfish harvesting, thereby creating more employment opportunities and social mobility (Michaelis et al., 2021 and Krause et al., 2020).

- Developing sustainable low trophic aquaculture and fisheries can provide job satisfaction by providing opportunities to work in the marine environment, enhancing people's sense of responsibility towards the stewardship of their environment, their waterfronts, and the many supporting local industries that benefit from the mariculture industry that provide stable accessible employment (Michaelis et al., 2021).
- Bivalve harvesting can promote food tourism, especially in more rural areas where high unemployment can push young workers towards more urban environments, often to the detriment of rural community cohesion (Urquhart & Acott, 2014).
- Seafood festivals not only promote the value of bivalves as food but also promote the local area as a marketing tool due to the desire of festival attendees to consume authentic local produce (Lee & Arcodia, 2011; van der Schatte Olivier et al., 2020).
- Poole Harbours fishing heritage is closely linked to its historic fisheries including the *O. edulis* fishery (Williams & Davies, 2018). Whilst production of *O. edulis* has declined over time, there is still a niche for high-value native species (Hambrey & Evans, 2016).
- Animal husbandry is a notable cultural service that differentiates aquaculture from fisheries. The role of bivalve caretakers can often attract non-fishermen industry participants that can boost social outreach and improve public opinion, in addition to influencing the development of the mariculture industry (Baines and Edwards, 2018; Michaelis et al., 2021).
- Additionally, shellfish harvesting can support other industries related to the food industry including tourism, vessel and gear maintenance, and artistic pursuits that improve community cohesion, invigorating local economies and wellbeing (Krause et al., 2019).
- Shellfish products like pearls and dyes have been associated with material wealth in various cultures, with bivalve shells inlayed into various objects including clothing, furniture, instruments, and even as a building material for cathedrals (Grant & Strand, 2019; Machado et al., 2020; Mannino & Thomas, 2023; Pinn, 2021; Warsh, 2018).
- Bivalves also provide value as leisure products as people often collect seashells for their artistic value when visiting the coast. Shell collection has been noted as an important activity for coastal populations and has a rich history of trade and collection, with major UK port cities exporting shells across the globe from designated shell collection centres throughout the 17th century (Dance, 1986).
- As discussed above in the Section 3, bivalve production can enhance other environments by improving water quality, reducing erosion, and rapidly cycling nutrients. This includes wild biogenic shellfish reefs and vegetative habitats such as seagrasses and salt marshes. These features support extensive biodiverse ecosystems which have their own substantial cultural value and services (Davidson 2019; de la Torre-Castro & Rönnbäck 2004; McKinley et al., 2018; zu Ermgassen et al., 2013).
- These habitats support recreational activities by increasing water quality and enhancing biodiversity. For example, recreational fishing which in addition to providing employment for charter vessels, also provide health and social benefits (Elliott et al., 2018).
- Research by Wheeler et al. (2015) suggests that people in the UK that live nearby or regularly visit the coast report better health and lower stress than populations who don’t, especially among socio-economically deprived areas where health conditions are more prevalent (Foster et al., 2018).
- Whilst water quality can indirectly impact tourism through enhancing biodiversity, water quality was noted historically to not appear to impact recreational activities such as fishing and swimming in England unless water quality is very visibly poor (Boeri et al., 2012; Ziv et al., 2016). This has changed over time with increasing instances of both bathing waters and shellfish waters being impacted by poor water quality. This can have consequences for public health as poor water quality can be associated with increased disease frequency and harmful algae blooms (Burge et al., 2016; Vantarakis 2021).
- Intensifying eutrophication can impact key species, particularly commercial demersal species such as flatfish and whelk, through food availability, shelter availability, and oxygen levels. Changes in the abundance and distribution of these species impact the maritime industry and the communities it supports (Engelhard et al., 2011; Casey et al. 2014; Rochette et al., 2010).

Summary of Section 4. Food Security

- In light of growing global food security concerns, aquaculture production has surpassed capture fisheries, producing 130 million tonnes in 2022 (FAO, 2024; Campbell et al., 2017). Of that figure, global bivalve mariculture produced 17.7 million tonnes, $29 billion annually (FAO, 2022).
- Despite this, UK per capita bivalve consumption (0.7 kg) lagged behind Portugal, France and Spain (4–8 kg) in 2022 (Willer & Aldridge, 2023). UK bivalve production has dropped by 62% since 2008, despite being recognised as a key sector in UK food security (DEFRA, 2015; Guillen & Virtanen, 2021)
- Surveys of British consumers linked this decline in bivalve consumption to taste, texture and preparation barriers (Willer et al., 2021). Bivalves are nutrient-rich, high in protein and omega-3s, with growing use in supplements (Grant & Strand, 2019; Tan et al., 2020).
- Bivalves are one of the few animals that are consumed whole, enabling micronutrient enhancement via the depuration stage (Lee et al., 2008; Willer & Aldridge, 2021). Bivalves have an added potential to address nutrient deficiencies including vitamin D deficiency, which 20% of UK population exhibit symptoms for (Lin et al., 2021; Sutherland et al., 2021).
- As low trophic-level feeders, mariculture bivalves do not require additional feed. If antibiotics are required, they are typically introduced in controlled hatcheries, reducing environmental impacts (Rana et al., 2009; Potts et al., 2021).
- In recognition on the value of bivalve aquaculture to food security, the UK Government aims to increase mussel production by 30,000 mt by 2040 (Huntington & Cappell, 2020).

- Poole Harbour aquaculture is primarily dominated by *M. edulis* (67%) and M. *gigas* (32%) (Huntington et al., 2023), with the Harbour aquaculture valued at £2.6 million (William & Davies, 2018).
- Poole Harbour hosts the largest *M. gigas* aquaculture operation in the UK. 95% of UK oyster fishery landings are *M. gigas*, valued at over £13 million in 2012. Landings have increased from 450 tonnes in 2011 to 1150 tonnes in 2021 (FAO, 2021; Humphreys et al., 2014 & 2021).
- Shellfish aquaculture supports rural coastal jobs, either directly or through economic linkages (Bonner-Thompson & McDowell, 2020; FAO, 2022). Bivalve beds can enhance wild fisheries via spat production and water quality improvements (Bishop et al., 2023).
- Aquaculture structures in the form of ropes and cages increase habitat complexity and biodiversity, benefiting fisheries (Mascorda-Cabre et al., 2021, 2023; Theuerkauf et al., 2022). To a lesser extent, on-bottom bivalve aquaculture also increases habitat complexity and biodiversity whilst rapidly cycling nutrients (McKindsey et al., 2007).
- Bivalve aquaculture has been shown to improve the resilience of vegetative habitats that act as fish nurseries for Plaice, pollock, herring and bass stocks (Bertelli & Unsworth, 2014; Green et al., 2009), especially in areas with high nutrient runoff such as Poole Harbour (Howarth et al., 2022).
- Poole Harbour's fisheries were valued at £9.9 million in 2017, whilst Poole's charter fleet had a £2 million turnover, employing fishers and supporting a range of associated businesses (Stebbings et al., 2020; Williams & Davies, 2018).

- Cultural benefits of aquaculture are hard to quantify but have visible communal and historical significance (Chan et al., 2012; Jones et al., 2016).
- As an important food source, bivalve harvesting shaped early human settlements, diet, art and tool use (Hausmann et al., 2021; Klein & Bird, 2016; van der Schatte Olivier et al., 2020). Bivalve shells have proven valuable in studying the deep past and informing on climate change (Klishko et al., 2020).
- Interviews with fishermen highlight how people in the industry see shellfisheries as a way of life rather than a job, increasing job satisfaction and supporting connections between identity, place and ownership (Krause et al., 2019; Urquhart & Acott, 2014).
- By providing environmentally sustainable employment by the sea, the industry can enhance a community's sense of environmental stewardship, and support local businesses, often in deprived rural coastal areas (Michaelis et al., 2021). Native species fisheries and seafood festivals promote the local area as a marketing tool in addition to aquaculture businesses, increasing tourism (Hambrey & Evans, 2016; Lee & Arcodia, 2011; Krause et al., 2019).
- Bivalve shells in particular have spiritual value and inspire artistic endeavours ranging from recreational beach walking for collecting, to use as a material for clothing and construction (Dance, 1986; Grant & Strand, 2019; Machado et al., 2020; Pinn, 2021).
- By enhancing water quality, bivalves can improve the resilience of seagrass beds and saltmarshes which in turn, provide their own cultural values (Davidson 2019; McKinley et al., 2018). In turn, healthier ecosystems and higher water quality support recreational water activities and associated industries that have human health benefits and social value (Elliott et al., 2018; Wheeler et al., 2015).

5. Potential Additional Ecosystem Services

- Depending on aquaculture operations, economic linkages and environmental conditions, bivalves provide a variety of ecosystem services. While not all of these services may apply in the current context of Poole Harbour, it is important to take them into account when assessing the overall benefits of the bivalve aquaculture chain.

5.1. Shell use

- Under current Poole Harbour aquaculture practices, lease beds are cleaned to improve relayed bivalve survival by removing blanketing macroalgae. Trawled solid sediment and fauna are returned to their harvested site at the earliest convenience to replenish the underlying habitat and avoid overexploitation of the ecosystem (Blake & zu Ermgassen, 2015).
- Poole Harbour fishermen typically sell bivalves alive or whole (personal comms with fishermen). Whilst this improves the value of sold meat, the fishermen rarely receive any added value from the potential uses of shell by-products, which make up the majority (up to 75%) of bivalve yield (Jović et al., 2019).
- Furthermore, the vast majority of sold shellfish go to the food industry where shells are frequently discarded as a waste product (Morris et al., 2019). As a result, there is a rising interest in recycling bivalve shells to reduce pollution associated with shell discards, driving greater awareness of the potential uses of shells as a raw material across multiple industries (Choi et al., 2024).
- Bivalve shells are primarily composed of calcium carbonate, a heavily versatile material with various industrial uses. Oyster shells have potential added value via the use of shells in construction through their addition to building composites.
- Separate studies by Ruslan et al. (2022) and Eziefula et al. (2018) provide evidence that integrating oyster shells into concrete significantly strengthens concrete. Adding shells reduces the demand for other raw materials with destructive extraction practices such as limestone and sand, thereby reducing the carbon footprint of infrastructure projects.
- A review of the uses of recycled mussel shells also highlights the use of mussel shells as substitutes for mortar and concrete components to improve formula strength (El Biriane & Barbachi, 2021).
- Oyster and mussel shells have also been used to enhance the water absorption properties and compressive strength of cement mortar resulting in a higher quality, more eco-friendly product (Song et al., 2022; Liao et al., 2022).
- Multiple medical applications have been identified for both oyster tissue in the form of Mytichitin CB peptides, and shell in the form of calcium oxide derived from calcium carbonate. These materials exhibit antimicrobial and antifungal properties, resulting in extensive industrial uses ranging from agricultural fungicides, medical equipment (Brakemi et al., 2024; Kim, 2022; Venier et al., 2019), and uses in food processing and packaging (Sadeghi et al., 2019).
- In addition to increasing the shelf life and agricultural output, a study by Lee et al. (2013) demonstrated that oyster shell extract exhibits anti-inflammatory properties by suppressing nitric oxide production. Other studies have highlighted other potential direct medical uses for oyster shells including shell-derived supplements that promote bone growth to treat a variety of skeletal conditions (Chaturvedi et al., 2013), and as a potent anti-fibrotic for scleroderma treatment (Latire et al., 2017).
- The antimicrobial properties of powdered shells have been studied for use in water purification, as oyster shell powder has been shown to absorb methylene blue and degrade organic matter (Jung et al., 2016). A study by Mignardi et al. (2024) recorded that hydroxyapatite, a material synthesised from manila clam shells, removed mercury ions (Hg^{2+}) from water at 94% efficiency over 40 minutes, further highlighting uses for bivalve shells in water purification.

- Bivalve shells are largely comprised of calcium carbonate, which when introduced to soil increases alkalinity, providing a buffer to soil acidity which can combat the overuse of fertiliser (Álvarez et al., 2012). Powdered shells can also be fed directly to farmed animals to supplement calcium carbonate in chicken feed to improve eggshell quality (van der Schatte Olivier et al., 2020).
- By combusting oyster shell at 700°C, the product can be used as a catalyst for the reaction that converts soybean oil and methanol to a viable form of biodiesel, with combusting brown algae showing potential as a catalyst for the production of synthetic natural gas (Choi et al., 2019; Nakatani et al., 2009).

Summary of Section 5. Potential Additional Ecosystem Services

- Bivalves provide various ecosystem services depending on shell use and tissue consumers. While not all apply to Poole Harbour, they are essential in assessing the broader benefits of bivalve aquaculture.
- In Poole Harbour lease beds are cleaned to improve bivalve growth and survival. During harvesting, market size bivalves are removed whilst sediment and fauna are returned to prevent habitat overexploitation (Blake & zu Ermgassen, 2015).
- Currently, bivalves are sold whole to retailers and restaurants. As a result, farmers gain no added value from shells, which can form up to 75% of total yield (Jović et al., 2019). Most shells end up as food industry waste, prompting a growing global demand for shell recycling to reduce waste and explore industrial applications (Choi et al., 2024; Morris et al., 2019).

- Calcium carbonate from oyster and mussel shells have been shown to enhance concrete strength whilst reducing reliance on materials like limestone and sand which have destructive harvesting methods with a high carbon footprint (El Biriane & Barbachi, 2021; Eziefula et al., 2018l; Ruslan et al., 2022)
- Additionally, shells have been shown to increase water absorption and compressive strength in cement mortar (Song et al., 2022; Liao et al., 2022).

- Bivalve shells have been shown to have multiple medical applications. Shell derived calcium oxide has been shown to have anti microbial and anti fungal properties , resulting in extensive industrial uses ranging from agricultural fungicides, medical equipment (Brakemi et al., 2024; Kim, 2022; Venier et al., 2019), and uses in food processing and packaging (Sadeghi et al., 2019).
- The antimicrobial properties of powdered shells have been studied for use in water purification, as oyster shell powder has been shown to degrade organic matter (Jung et al., 2016)
- Hydroxyapatite is a material synthesised from manila clam shells that has been shown to remove mercury ions (Hg2+) from water at 94% efficiency over 40 minutes (Mignardi et al., 2024).
- Oyster shell extract shows Anti-inflammatory properties and potential in bone growth supplements to help treat a variety of skeletal conditions (Lee et al., 2013; Chaturvedi et al., 2013; Latire et al., 2017).

- Bivalve shells also show promise for agricultural applications. Powdered shells have been fed directly to farmed animals to supplement calcium carbonate in chicken feed to improve eggshell quality (van der Schatte Olivier et al., 2020).
- A study by Álvarez et al. (2012) highlights the value of bivalve shells as a soil pH buffer as the alkaline calcium carbonate can counteract the overuse of acidic fertilisers.
- By combusting oyster shell at 700°C, the product can be used as a catalyst for the reaction that converts soybean oil and methanol to a viable form of biodiesel, with combusting brown algae showing potential as a catalyst for the production of synthetic natural gas (Choi et al., 2019; Nakatani et al., 2009).

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