Ecosystem engineers enhance the multifunctionality of an urban novel ecosystem: population persistence and ecosystem resilience since the 1980s

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Graphical Abstract

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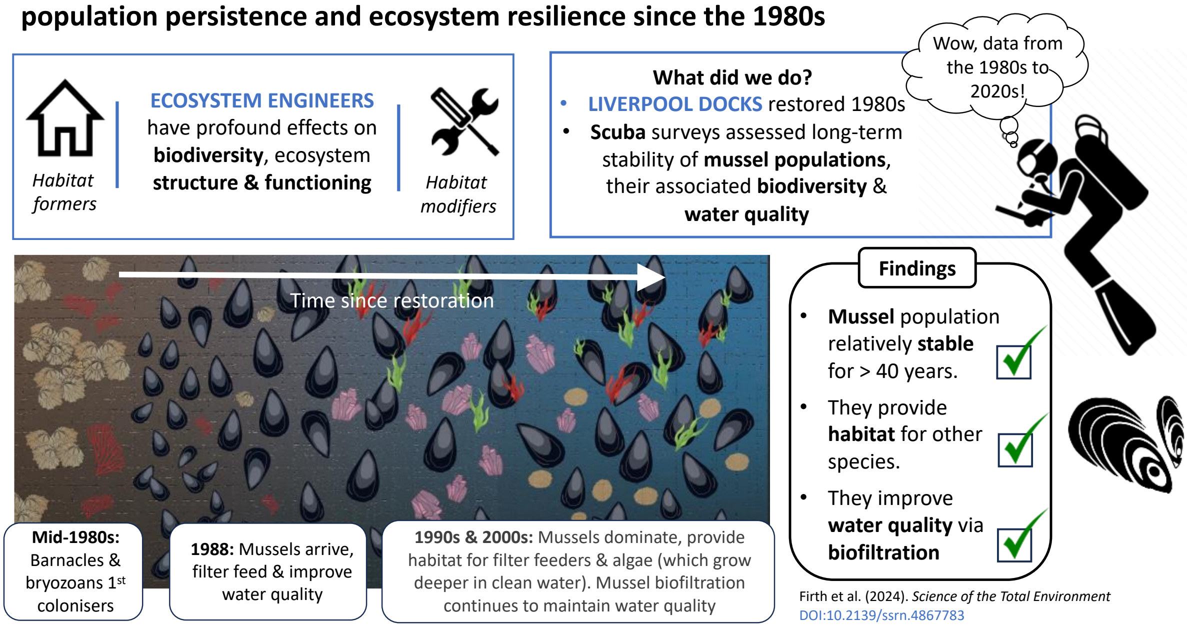

Abstract

In degraded urban habitats, nature-based solutions aim to enhance ecosystem functioning and service provision. Bivalves are increasingly reintroduced to urban environments to enhance water quality through biofiltration, yet their long-term sustainability remains uncertain. Following the restoration of the disused South Docks in Liverpool in the 1980s, natural colonization of mussels rapidly improved dock-basin water quality and supported diverse taxa, including other filter feeders. While the initial colonization phase has been well documented, there has been limited published research since the mid-1990s, despite ongoing routine water quality monitoring. Here, we assessed the long-term persistence of mussel populations, their associated biodiversity, and physico-chemical parameters of the water in Queens and Albert Docks by comparing historical (1980s to 1990s) and contemporary data from follow-up surveys (2012, 2022). Following an initial period of poor water quality (high contamination and turbidity, low oxygen), the natural colonization of mussels from Albert Dock in 1988 extended throughout the South Docks. By the mid-1990s, the environment of the South Docks and its mussel populations had stabilized. The dock walls were dominated by mussels which provided important complex secondary substrate for invertebrates and macroalgae. Surveys conducted in 2012 and 2022 confirmed the continued dominance of mussels and estimates of mussel biofiltration rates confirm that mussels are continuing to contribute to maintaining water quality. A decline in salinity was observed in both docks in 2022, with evidence of recovery. While these ecosystems appear relatively stable, careful management of the hydrological regime is crucial to ensuring the persistence of mussels and resilient ecosystem service provision through biofiltration.

Keywords

Urban regeneration, biofiltration, water quality, ecosystem services, restoration, biodiversity, sustainable development

Introduction

Climate change and urbanization are driving the 'artificialisation' of the global coastline (Bugnot et al. 2021). Coastal built environments that support human activities (e.g., harbours, marinas, artificial islands) are replacing natural habitats with cascading negative environmental impacts (Airoldi et al., 2021; Dafforn et al., 2015). The resultant marine built environments have been likened to 'novel ecosystems' (Bulleri et al., 2020) because they have been deflected irrevocably from their historical trajectories. While these ecosystems have no natural counterparts, they can become biodiversity oases in urban areas (Seitz et al., 2022; Lemasson et al., 2024) and provide essential ecosystem services (Hobbs et al., 2009). A deeper understanding of their biodiversity and ecosystem processes can enhance the effectiveness of multifunctional approaches to urban ecosystem service provision (Soga and Gaston, 2018). Research that identifies minor interventions for rehabilitating these systems and management strategies is critical for ensuring their long-term viability.

The global urbanization of estuaries has led to the conversion of millions of hectares of mudflats and wetlands into reclaimed land with associated engineered infrastructure, such as seawalls, groynes, wharves, dock basins, and piers (Chee et al., 2017; Bugnot et al., 2021; Firth et al., 2024). These artificial structures support diverse marine benthic communities, although they often have lower native biodiversity and higher invasive biodiversity compared to natural habitats (Firth et al., 2013; O'Shaughnessy et al., 2020, 2023; Jackson-Bué et al., 2023). In heavily modified urban areas, it is impractical or impossible to restore them to their pre-disturbance state (Hobbs et al., 2009). In such contexts, Nature-based Solutions (NbS), such as greening grey infrastructure (GGI), offer a pragmatic approach to optimizing ecosystem functioning without attempting to restore natural habitats (Strain et al., 2018; Evans et al., 2021). By implementing GGI, multiple ecosystem processes can be enhanced to ensure the provision of services to society within novel ecosystems, without compromising their human utility (Rosenzweig, 2003).

To date, GGI projects have largely followed a non-specific "build it and they will come" approach, relying on natural recruitment (O'Shaughnessy et al., 2020; Evans et al., 2021; Bishop et al., 2022). However, there is growing interest in transplanting desirable ecosystem engineers onto artificial marine habitats to establish biogenic structures, expedite facilitation cascades, and enhance ecosystem processes that deliver services to society (Strain et al., 2021; Chee et al., 2021; O'Shaughnessy et al., 2021). For example, the Billion Oyster Project aims to improve water quality in New York Harbor by creating a 100-acre oyster reef by 2030 (Janis et al., 2016). Researchers are using artificial structures, such as bulkheads and gabions, to successfully install oysters (www.billionoysterproject.org). Similarly, integrating breakwaters with oyster restoration structures can improve the structural and ecological performance of living shorelines along dynamic coastlines (Safak et al., 2020), though significant uncertainties remain (Morris et al., 2019, 2021). These initiatives often rely on short-term studies, typically lasting less than five years (Bayraktarov et al., 2016; Evans et al., 2021), but the long-term outcomes can differ (Rezek et al., 2019). Therefore, the long-term efficacy of restoration, rehabilitation, and reconciliation initiatives should be evaluated through transgenerational ecological surveys spanning decades (Hawkins et al., 2013; Mieszkowska et al., 2014).

The waterfront of Liverpool, UK, presents a unique opportunity to evaluate the long-term performance of ecosystem engineers and their service provision in a novel urban ecosystem. The macro-tidal Mersey Estuary has been reshaped by 300 years of port infrastructure development, including seawalls, enclosed dock basins accessed via lock gates, jetties, quays, and a major ship canal—much of which later experienced economic decline and disuse (Figure 1a, Ritchie-Noakes, 1984). The Liverpool South Dock complex became increasingly redundant after World War II as ships grew larger, a fate common among traditional ports on the UK's macro-tidal estuaries and navigable inland waters (Hawkins et al., 1992a; Williams, 2005). After their closure, the dock gates were left open, leading to the docks silting up (Figure 1a, Hawkins et al., 1992a; Hawkins et al., 1999). Urban regeneration in Liverpool focused on the waterfront buildings and dock warehouses (Figure 1b). The health and attractiveness of the aquatic ecosystems in the dock basins were crucial to the success of the surrounding restored and repurposed warehouse buildings. Initially, however, the water quality was very poor. These initiatives were particularly challenging given that the Mersey was one of the most polluted catchments and estuaries in the UK and Europe, necessitating a massive clean-up campaign from the 1980s onwards (see Hawkins et al., 2020 for review).

Early initiatives included mussel aquaculture in Sandon Dock (Hawkins et al., 1992a, b). The top-down biofiltration by mussels on ropes and dock walls, combined with bottom-up artificial mixing via an air lift pump, significantly improved water quality (Russell et al., 1983). These lessons were then applied to managing the poor water quality in the South Docks complex, centred around the iconic Albert Dock, which underwent redevelopment including dredging and water replacement between 1981 and 1985. A critical factor in the rapid water quality improvement of the South Docks was the natural colonization of dense mussel (*Mytilus* spp.) populations on the dock walls, acting as biofilters and secondary habitat for a wide range of species (Figure 1c,d, Allen et al., 1992; Allen and Hawkins, 1993; Wilkinson et al., 1996). Revisiting this novel ecosystem provides invaluable insights into the long-term performance of rehabilitation projects, particularly highlighting the role of top-down control through bivalve biofiltration and the manipulation of bottom-up processes through mixing.

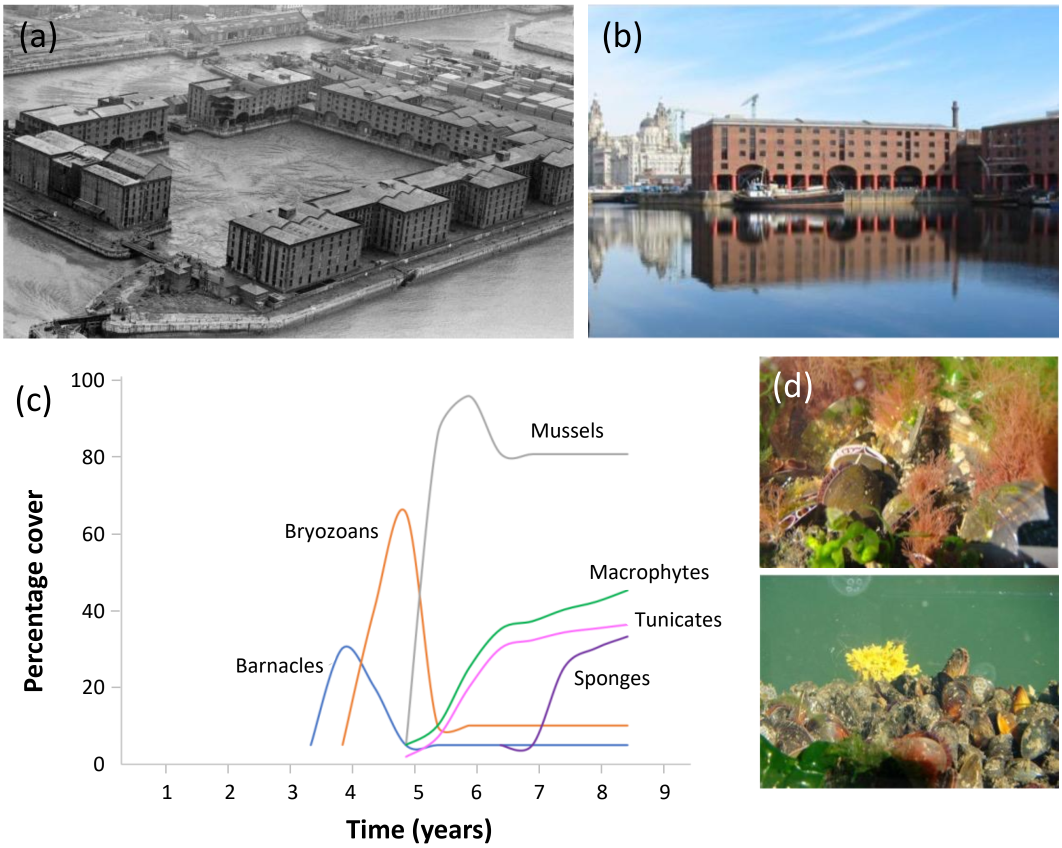

Figure 1. The Liverpool Docks: an urban novel ecosystem. (a) The Albert Dock full of silt prior to dredging and restoration work in 1980. (b) The Albert Dock in 2012 – part of the then Liverpool Maritime Mercantile City UNESCO World Heritage Site (lost UNESCO status in 2021). (c) Schematic diagram showing colonisation of major biotic groups on the walls in the Albert Dock following dredging and refilling with water. Dredging and replacement with water occurred between 1981 and 1985. Water quality remained relatively poor until a dense natural settlement of mussels occurred in late summer and autumn of 1988. Figure modified from Hawkins et al. (1999) and Allen (1992). (d) Images of diverse epibiotic communities living on dense mussels on the dock walls. Image credits: a = Copyright unknown; b and d = Louise Firth.

This study comprises a 40-year case study of the benthic ecosystems in the redundant Liverpool Docks. Our overarching goal was to assess the long-term stability of benthic communities on the dock walls, thereby evaluating the structural persistence and functional resilience of this novel ecosystem. Focusing on Albert and Queens Docks, we combined historical data from the 1980s and 1990s, including both published and unpublished sources (such as theses and consultancy reports, Table S1), with data from targeted re-surveys conducted in 2012 and 2022. Our specific objectives were to:

(1) Quantify the extent of novel habitats and built land.

(2) Describe changes in the physico-chemical parameters of the water.

(3) Quantify the changes in cover and population structure of mussels (*Mytilus* spp.), the key ecosystem engineers in this system.

(4) Chart long-term successional changes in the associated benthic assemblage.

(5) Estimate contemporary biofiltration rates by mussels.

Materials and Methods

Study system: the Liverpool South Dock Complex

Docks were constructed along both sides of the Mersey River starting in the early 18th century, leading to the narrowing and 'hardening' of the outer Mersey Estuary (Figure 2). On the east bank, extending from Liverpool City Centre, the docks stretched approximately 11.5 km from Dingle in the south to Crosby in the north. On the west bank, the Wirral Docks extended about 2.5 km on either side of Birkenhead.

In 1981, a major urban renewal scheme focused on the derelict South Dock complex (Figure 2; see Hawkins et al., 1992b, 2020 for comprehensive reviews). When the dock gates were restored in 1984 and water reintroduced, the area was prepared for the restoration and repurposing of warehouses for commercial, cultural, residential, and touristic use (Hawkins et al., 1999). Initially, the dock basins contained stagnant, oxygen-poor, and heavily polluted shallow water with dense algal blooms (Hendry et al., 1988; Allen et al., 1992, 1995; Hawkins et al., 1992a). This situation prompted research on water quality improvement and ecological rehabilitation. In a 1988 pilot trial, based on earlier work in Sandon Dock (Russell et al., 1983), an airlift pump was installed to mix the water column and prevent the formation of a thermocline. Mussels (*Mytilus* spp.) were imported from the Menai Straits and grown in suspended culture, supplemented by mussels scraped from navigational buoys. The aim was to test if this rehabilitation approach would work throughout the South Docks. The Royal Albert Dock (hereafter Albert Dock) was designated as a mussel-free control dock. In 1988, a dense natural settlement of mussels fortuitously occurred (Allen et al., 1992), likely due to the opening of the lock gates to allow ships and water from the River Mersey to enter during the Tall Ships Race, eliminating the need for further human intervention. This settlement was heavier in Albert Dock than in the other docks, including Queens Dock, indicating that the Mersey was the source rather than the transplanted mussels in Graving Dock.

Figure 2. Map of the Liverpool Docks on the east side of the River Mersey. Insets show the area of the docks within the city of Liverpool and the wider UK. Main map shows locations that are mentioned in this paper. South Docks encompass everything southward of the Three Graces, and the North Docks encompass everything northward of the Three Graces.

Following the dredging and clean-up of the docks, annual surveys of physico-chemical conditions and biodiversity were conducted from 1988 to 1996 (see Table S1 for summary). Initially, the pioneering sessile community was dominated by barnacles and bryozoans. However, the dense natural settlement of mussels in 1988 shifted the community structure to mussel domination, which persists to the present day (2024, Mieszkowska, pers. obs.). The mussels not only improved water quality but also created complex habitats for associated flora and fauna, including tunicates, sponges, macrophytes, and smaller organisms such as amphipods and polychaetes (Figure 1c, Allen et al., 1995; Wilkinson et al., 1996).

From 1988 to 1990, water quality improvements in Albert Dock were achieved solely through mussel biofiltration, without the need for mechanical mixing (Hawkins et al., 1992; Allen et al., 1992; Allen and Hawkins, 1993). Anticipating the increased likelihood of water stratification due to early concerns about global warming in the 1990s, one of the authors (JRA) designed a low-cost perforated-pipe compressed air mixer. This mixer lay along the bottom of Albert Dock, avoiding interference with navigation, unlike Helixor-type mixers that stood above the dock bottom. This system was used as needed until at least 1996, guided by routine temperature and oxygen profile measurements.

In the mid and early 1990s, the combined natural biofiltration by mussels colonizing the walls of Albert Dock, supplemented by artificial mixing from an airlift pump, significantly enhanced and sustained water quality and clarity (reviewed in Hawkins et al., 2020). This improvement allowed algae to thrive deeper in clearer waters, while bivalves and other benthic invertebrates colonized the dock walls down to the sediment depths (Hawkins et al., 1993; Allen et al., 1995). Following this research phase, monitoring transitioned to routine water quality assessments conducted by consulting firms. Despite these improvements, sediment colonization remained limited, characterized by glutinous, anoxic mud. Overall, the transformation resulted in a diverse and entirely novel community on the dock walls, leading to lower phytoplankton populations, clearer water, and reduced anoxia in enclosed and deeper basins. Given the dominance of wind mixing in shallower and larger docks, artificial mixing was unnecessary and impractical. Mussels proliferated across these docks, covering the walls extensively. In 2009, a significant alteration to navigation occurred with the connection of the freshwater Leeds-Liverpool Canal to Princes Dock, extending into Canning and the South Docks.

Quantification of extent of novel habitats and built land

The extent of built land and novel habitats resulting from dock construction was assessed from Crosby Beach in the north to the now infilled Harrington Dock in the south (Figure 1). The infilled Herculaneum Dock was excluded from this assessment because sections of the foreshore bedrock were cut back rather than new land being created for its construction (Ritchie-Noakes, 1984). Novel habitats encompassed permanently submerged vertical seawalls and muddy bottoms in enclosed areas unaffected by tidal flows but subject to non-tidal fluctuating water levels due to locking and water exchange.

The extent of newly built land was determined by comparing historic maps from the 15th to 19th centuries with modern maps. The historic coastline of Liverpool was digitized onto modern Ordnance Survey base maps and replicated in Google Earth Pro using aerial imagery from April 2020. This process allowed for the digitization and quantification of both the coastline and internal waters within the newly developed areas. In addition to permanent novel habitats, the area covered floating pontoons, was also assessed by multiplying the total linear extent of the pontoons (both sides) by 0.5 m — the depth at which pontoons typically sit below the water surface.

Physico-chemical parameters

Physico-chemical data were collected at various intervals throughout the study period (see Table S1 for summary). Historical data were compiled from a range of published and unpublished sources, including MSc and PhD theses (Table S1), while more recent data were gathered by environmental consultancies between 2005 and 2014, as well as during planned resurveys in 2012 and 2022. Using a multiprobe system, sea water temperature (°C), dissolved oxygen (DO, mg/L), and salinity (ppt) were measured monthly (sometimes thrice monthly) at the surface and at 1-m intervals down to the dock bottom in both Albert and Queens Docks.

Water clarity was assessed using Secchi extinction depth, with a minimum clarity depth of >2 m considered as the standard, surpassing the >1 m guidance outlined by the European Commission Bathing Water Directive of 1975. Chlorophyll-a levels were determined from one-litre samples collected just below the water surface. Only data from the summer months (June to August) of each year were included due to data availability. Efforts primarily focused on periods when water quality issues like anoxia and algal blooms—often linked to water column stratification—were more likely to occur. Differences in physico-chemical variables were tested using Two-Factor

PERMANOVA with Factors Dock (Albert, Queens; fixed factor) and Year (various, fixed, orthogonal). To restrict comparisons to overall trends, depth was not included as a factor in the statistical analysis but is maintained in the figures. Univariate PERMANOVA was chosen for univariate analyses because it allows for two-factor designs, considers an interaction term and does not assume a normal distribution of errors. The tests were run on Euclidean distances matrices with 9999 permutations (Anderson, 2001).

Mussel population density and structure in Queens and Albert Docks

Historical data spanning 1989 to 1996 were gathered from a variety of published and unpublished sources, while re-surveys were conducted in 2012 and 2022 (see Table S1 for data collection details across years and docks).

Except for 2022, mussel population density and structure data were collected using identical methodology. For surveys conducted between 1989-1996 and 2012 SCUBA divers scraped all mussels within 0.25 m × 0.25 m quadrats (3-5 replicates) into net bags (1 mm mesh size) along at least two vertical transects per dock. Due to restrictions on SCUBA diving in the docks, in July 2022, mussels were scraped from 0.25 m × 0.25 m areas with a hoe and collected in a net (1 mm mesh size) held below the quadrat being sampled. For all surveys, the density and length of each mussel in every quadrat were measured using dial callipers accurate to 0.1 mm.

From 1989 to 1996, annual samples were collected at depths of 1 to 2 m in Albert and Queens Docks during the summer months (July/August). In 2012, samples were taken during both winter and summer. In February 2012, surface samples were collected from both Albert and Queens Docks, including just below the surface on floating pontoons in Albert Dock. In August 2012, samples were gathered at 1 m depth intervals in Albert Dock (surface, 1, 2, 3, 4 m, and pontoons) and in Queens Dock (surface, 1, 2 m).

Raw data were not available for the historical surveys; thus, data were mined from graphs using Image J (Schneider et al., 2012). Comparison of mussel length data among years was tested using Kolmogorov-Smirnov (K-S) Tests.

Mussel cover and associated benthic assemblage structure

Historical data from 1989 and 1992 regarding mussel percentage cover and the associated benthic assemblages were extracted from Allen (1992) and Wilkinson (1995) while re-survey data were collected in 2012 only. In all surveys, SCUBA divers captured non-destructive photo quadrats (0.25 m × 0.25 m) of mussels and their associated epibionts at 1 m depth intervals (see Table S1 for details).

Raw data were not available for the historical surveys; thus, data were mined from graphs using Image J (Schneider et al., 2012). In 2012, images were analyzed using Image J (Schneider et al., 2012) to quantify the percentage cover of major species and functional groups. Photographs with poor visibility or unidentifiable biota were excluded from the final dataset. A minimum of 10 replicate photographs was analysed for each depth interval. Due to the lack of raw data from historical surveys, information was extracted from graphs and tables in theses and papers, also utilizing

Image J. To assess differences in multivariate taxonomic composition, PERMANOVA was employed, conducting 9999 unrestricted permutations of raw presence/absence data from the 2012 dataset only (Clarke and Warwick, 1994).

To assess both micro- and macro-algal communities, a single hand-grabbed sample of algae was collected from each specified depth (Queens Dock: surface, 1, 2, 3, 4 m; Albert Dock: surface, 1, 2 m) and preserved in plastic bottles. In the laboratory, all samples underwent identification to the lowest possible taxonomic level using Zeiss Axio Imager A2 and Zeiss Axioscop microscopes. Upon initial examination and enumeration of fresh samples, each sample was then treated sequentially with 34 % hydrochloric acid to dissolve carbonates, followed by 70 % nitric acid. After boiling for 10 minutes and allowing to settle for 24 h, samples were rinsed ten times with distilled water to neutralize acidity. Suspensions were then dried onto cover slips for light microscopy (LM) and mounted in Naphrax. Diatoms were identified to species using a Zeiss Axio Imager A2 microscope equipped with differential interference contrast and plan apochromat objectives. No formal statistical comparisons were conducted on the algal communities.

Estimation of mussel clearance rates

Given the level of importance that has been given to the role of mussel biofiltration in underpinning improved water quality in this system in the past (Wilkinson et al. 1996), we considered it important to provide a contemporary estimate of clearance rates and to compare them between across habitats (pontoons, dock walls), docks (Albert, Queens) and depths. We acknowledge that clearance rates depend not only on mussel weight but also on mussel density, water quality and current speed; hence, we advise that these calculations be viewed with caution. Wet weight of a haphadardly selected proportion (~80 %) of mussels from each quadrat was measured, and ash-free dry weight (AFDW) of the soft tissue (±0.0001g) determined following drying of individual mussels at 70 ºC for 48 h or until constant mass achieved (Knights, 2012).

A rough general estimation of clearance rate (CR) of mussels based on body mass (g ash free dry weight; AFDW) was previously described by Smaal et al. (1986) and applied in two previous studies of Liverpool docks (Allen et al. 1992; Wilkinson et al. 1996). Estimates of individual mussel CR were calculated as:

CR_{INDIV} (l h^{-1} individual^{-1}) = $1.647 \cdot W^{0.61}$ [1]

where W is g AFDW of tissue.

CR_{INDIV} data were then scaled-up to a 'patch' estimate, coupling individual CR with survey estimates of mean mussel density per m^2 (D) as follows:

CR_{PATCH} (l h^{-1} m^{-2}) = $CR_{INDIV} \times D$ [2]

Variation in CR_{PATCH} was also estimated by as mean D ± the standard deviation in density among quadrats. We tested for differences in CR_{INDIV} among locations and sampling depth using two-factor analysis of variance performed in R (R Core Team, 2024).

Results

Extent of novel habitats and built land in the South Dock complex

The construction of the Liverpool Dock complex on the east bank of the Mersey (spanning from Crosby Beach in the north to the infilled Herculaneum Dock in the south) resulted in the development of 664 ha of new land. This includes 218 ha of continuously submerged dock basins and over 11 km of seawalls beyond the docks exposed to regular tidal cycles (Figure 2). Specifically, the South Docks alone account for 136 ha of constructed land, featuring 28.2 ha of dock basins and 3.2 ha of newly submerged seawalls within the docks. Additionally, the installation of floating pontoons in some docks has introduced an extra 0.4 ha of new floating habitat (Table S2). The variations in depth, surface area, proximity to Mersey inflows, and the recent connection to the Leeds Liverpool Canal in 2009 have created a mosaic of similar yet slightly distinct standing water environments that support diverse biological communities.

Physico-chemical parameters

All physico-chemical variables differed significantly over time but only some differed between docks (Table 1). While there was a significant main effect of Year, temperature fluctuated over time and no clear trends or patterns emerged (Figure 3a). Notably, the warming trends observed in the waters surrounding the British Isles post-1988 were not evident within the docks. Overall, temperature was significantly higher in Queens Dock (average 18.8°C) compared to Albert Dock (18.0°C). Being deeper than Queens Dock (<4 m), Albert Dock (<6 m) is more prone to natural thermal stratification (Figure 3a, Table 1). From 1991 onwards, Albert Dock was artificially mixed in summer using an airlift device, which mitigated stratification. In 1994, operational issues with the device led to stratification (Wanstall, 1997). In recent years, the device has not been used and was removed in 2022 (A. Goodey, Canals and Rivers Trust, pers. comm.). Summer surface temperatures consistently exceeded bottom temperatures in Albert Dock, with wider surface standard errors indicating occasional stratification. Conversely, differences between surface and bottom temperatures were generally smaller in Queens Dock, reflecting its shallower, more open nature conducive to wind mixing. In 2022, surface temperatures in Queens Dock were slightly lower than bottom temperatures, indicating cooler freshwater resting above slightly warmer saline water (as evidenced in salinity differences, Figure 3b).

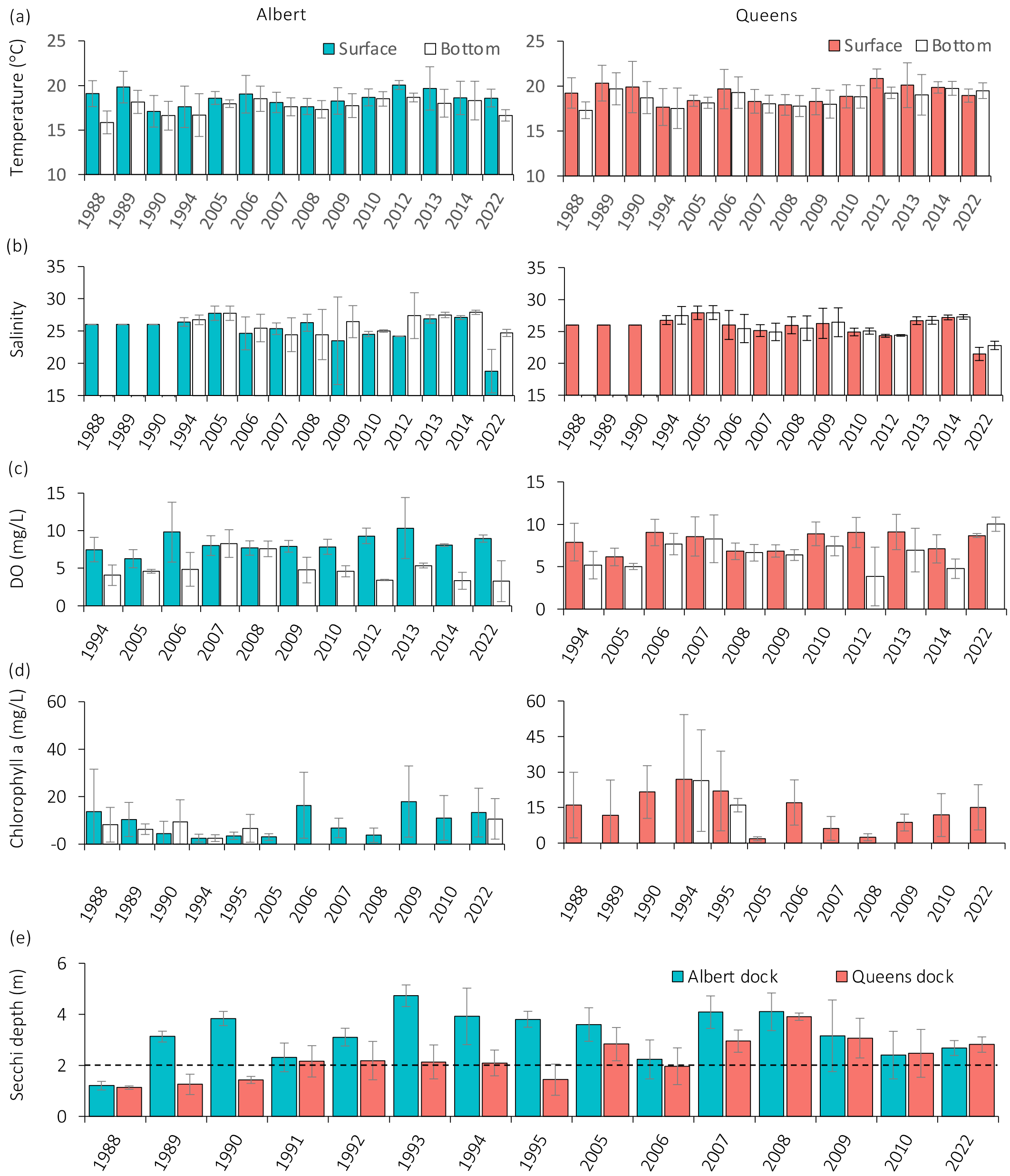

Figure 3. Variation in physico-chemical parameters in the summer months (June-August) in Albert Dock (blue) and Queens Dock (pink) between 1988 and 2022 (mean values ± S.E.). (a) temperature (°C); (b) salinity; (c) dissolved oxygen (DO, mg/L); (d) chlorophyll a (mg/L) (e); and water clarity depth (m). All parameters except water depth are given for the surface and 1 m above the bottom in each year. The dashed line in (e) indicates the >2 m minimum standard clarity depth. See Table S1 for details

on data sources. Not all parameters were measured in all years. Note that salinity for 1998-1990 was simply reported as 24-28 (Allen, 1992).

There was a significant main effect of Year on salinity (Table 1). In all years sampled average summer salinity was consistently above 24 in both docks. In 2022, there was a significant reduction in salinity (PERMANOVA, post hoc comparisons) and this was observed in both Albert and Queens Docks. In Albert Dock, surface salinities consistently remained below 22, reaching a low of 11 in July due to heavy rainfall and runoff. Slightly higher salinities (17.6 and 21.4) were observed during the two sampling events in August, suggesting possible recovery. A similar albeit less pronounced decrease was noted in Queens Dock (consistently below 23, with a low of 19.4), suggesting that the closer proximity of Albert Dock to the freshwater input of the Leeds-Liverpool Canal may be a factor driving the lower salinities observed.

There was a significant main effect of Year for dissolved oxygen and significant interaction between Dock and Year for Chlorophyll a (Table 1). Typically, dissolved oxygen levels were higher at the surface (always above 5 mg/L) than at the bottom (often below 5 mg/L) across most years, but no other trends were obvious (Figure 3c). No discernible trends were evident for Chlorophyll a (Figure 3d).

There was a significant interaction between Dock and Year for water clarity (Table 1). Initially, in 1988, water clarity was similar in Albert and Queens Docks (~1.1 m), falling below the minimum 2 m clarity standard. Water clarity in Albert Dock was significantly deeper than Queens Dock for seven of the fifteen survey years (PERMANOVA, post hoc comparisons: 1989, 1990, 1992, 1993, 1994, 1995, 2007). In Albert Dock, the only clear temporal trend was that water clarity was significantly shallower in 1988 compared to all other years. From 1989 onwards, mean water clarity in Albert Dock consistently exceeded 2.2 m, averaging 3.2 m annually. Conversely, water clarity in Queens Dock remained consistently shallower than in Albert Dock during the early years (often around or below 2 m until 1995; PERMANOVA, post hoc comparisons). From 2008 onwards, water clarity depths increased (>2 m) and became more similar between both docks and years, possibly due to increased boat traffic and sediment disturbance following the Leeds-Liverpool Canal connection.

Mussel population structure and growth in Queens and Albert Docks

Natural recruitment of mussels on the walls of both Albert and Queens Docks began in 1988, four years after the dock-gates were reinstated and water retention began. Initially, Albert Dock experienced very high densities (>4000/m^2 in both 1989 and 1990) due to a substantial recruitment event in summer/autumn 1988, likely originating from the Mersey. In contrast, Queens Dock had lower densities (<1000/m^2), possibly indicating a different route of recruitment or a lack of water flow between Albert Dock (which is closer to the lock gate) and Queens Dock. Albert Dock's mussel densities declined sharply over a 2-year period to around 1200/m^2 by 1991, followed by a gradual decrease until stabilizing in the mid-1990s. Since 1995, densities have fluctuated between a low of 53/m^2 in 1996 and a high of 224/m^2 in 2012. In Queens Dock, densities were consistently lower than Albert's in the early years (always below 1000/m^2). From 1992 onwards, densities have been similar, varying between a low of 120/m^2 in 1995 and a peak of 350/m^2 in 2012.

Between 1989 and 1992/1993, the mean length of mussels in both docks increased (Figure 4a), stabilizing around 50-60 mm. Initially, mussels were smaller in Albert Dock, likely due to intense intraspecific competition. However, since 1992, they have consistently been larger than those in Queens Dock. By 2022, both docks experienced a significant decline in mean mussel length: Queens Dock decreased from 48 mm in 2012 to 10 mm in 2022, while Albert Dock dropped from 66 mm in 2012 to 47 mm in 2022.

The mussel population structure in both Albert and Queens Docks evolved over time. Albert Dock underwent a rapid shift from a size structure dominated by recruits (<20 mm length) to larger mussels between 1989 and 1992 (Figure 4b, K-S Tests, $P < 0.05$), driven by the initial massive colonizing cohort. From 1992 to 2012, although the median size continued to increase (not significant, all K-S Tests, $P > 0.01$), indicating sustained growth of the initial cohort. However, by 2022, the median size had significantly decreased (~47 mm) compared to 2012 (~62 mm) (K-S Test, $P < 0.05$).

Queens Dock exhibited a different pattern (Figure 4c). Recruitment was slower initially, but following a strong event in 1992, the population remained relatively stable from 1992 to 1996. By 2012, the population structure had reverted to earlier patterns, indicating possible recruitment events in the interim. Like Albert Dock, in 2022, the median size was significantly (K-S Test, $P < 0.05$) smaller (~10 mm) than in 2012 (~53 mm).

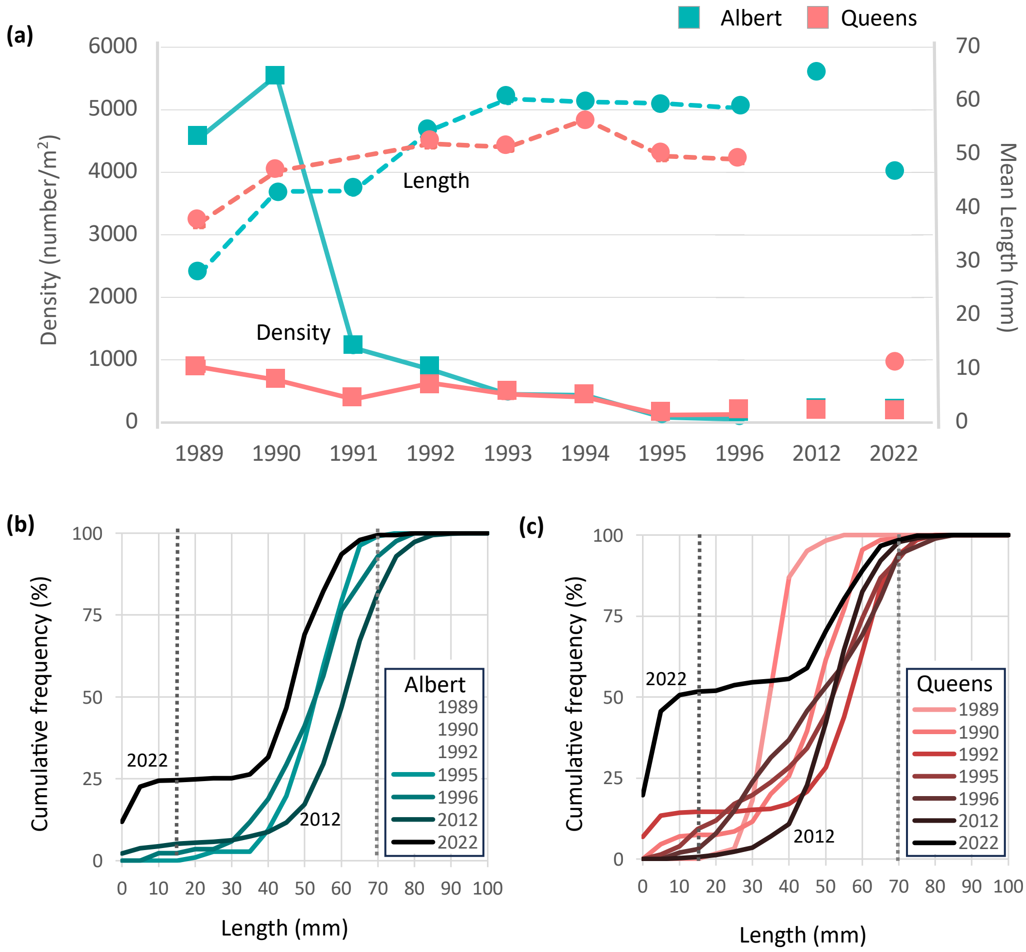

Figure 4. Mussel population structure and growth. (a) Mean density (continuous line) and mean length (dashed line) of mussels at 1 to 2 m depth in Albert and Queens Docks in summer 1989-1996 (annual sampling), 2012 and 2022 (single year samples). Mussel length cumulative frequency curves from selected years in (b) Albert and (c) Queens Docks. The dotted grey lines at 15 mm and 70 mm indicate the percentage of population which may be recent recruits and those that are 'very large' respectively. Samples were taken at a depth of 2 m. Blue = Albert; pink = Queens.

Surveys in 2012 indicated that mussel recruitment was observed at all depths in Albert Dock, with the highest recruitment found at 3 to 4 m depth and the lowest near the surface, possibly due to mortality linked to fluctuating water levels (Figure 5a). Median mussel size showed a slight tendency to decrease with depth in both docks (Figure 5a).

Recruitment on a newly installed pontoon in February 2012 was higher compared to the dock wall (Figure 5b), suggesting that intraspecific preemptive competition for space may have hindered recruitment on the wall. Subsequent surveys of the pontoons showed rapid growth, with median length increasing from 27 mm in February to 38 mm in August. In contrast, median mussel lengths on the dock walls only increased from 63 to 66 mm in Albert Dock and 52 to 58 mm in Queens Dock.

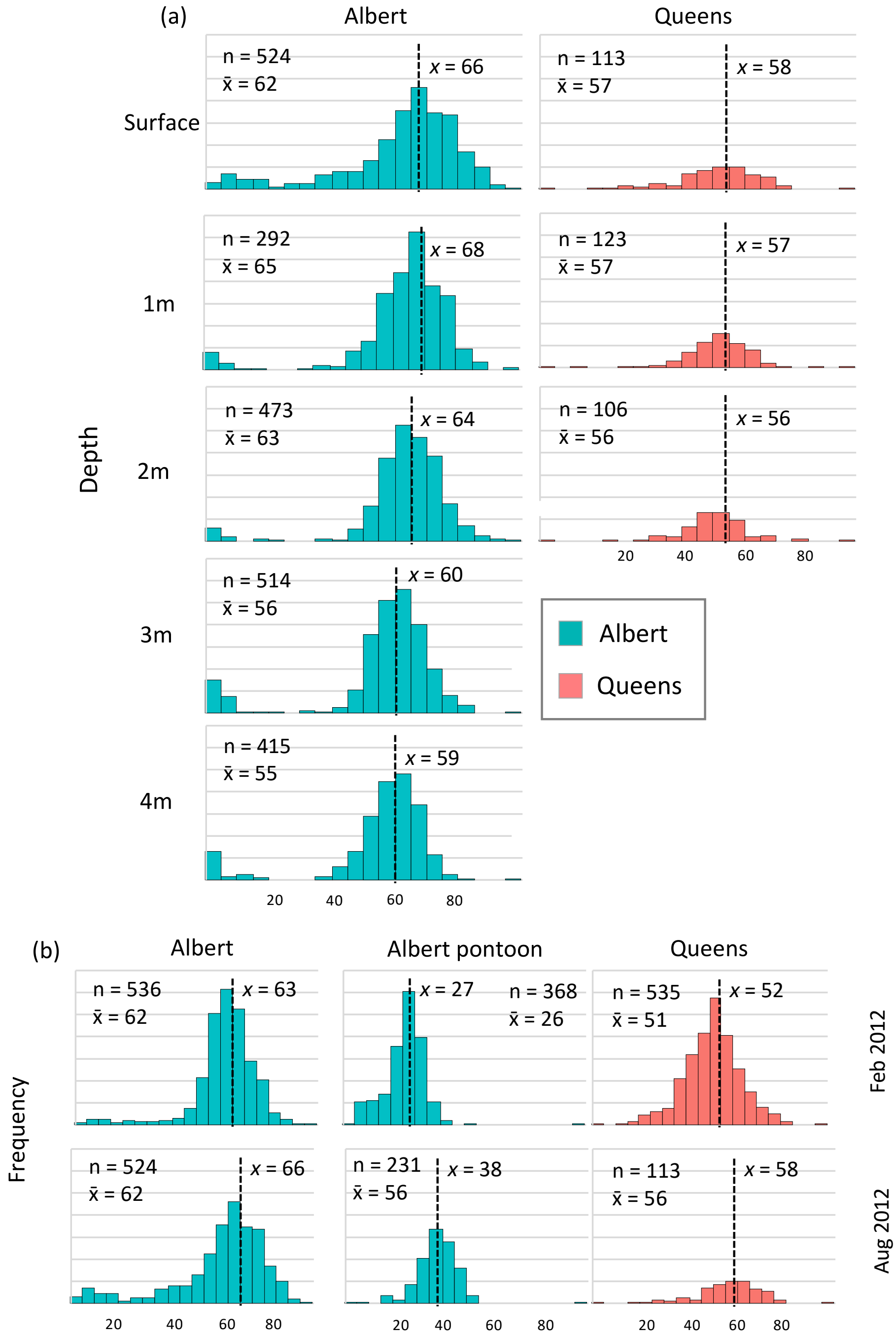

Figure 5. Length frequency histograms of *Mytilus* spp. populations in Albert and Queens Docks; (a) Depth gradient in 2012 and (b) Six months of mussel growth at the surface and on the pontoons between February and August 2012. Blue = Albert; pink = Queens.

Benthic assemblage associated with mussels in Albert and Queens Docks

Mussel percentage cover in both docks typically showed lower values at the surface, likely due to fluctuating water levels, and at the dock floor across all sampled years (Figure 6). In Albert Dock, mussel cover fluctuated widely over time, peaking at around 75 % in 1989 and dropping to a low of 19 % in 1995 (Fielding, 1995, not shown in Figure 6). By 2012, mussel cover had rebounded to 56 % in Queens Dock and 55 % in Albert Dock (PERMANOVA, $P > 0.05$).

Initially, the epifaunal community was dominated by bryozoans in both Queens and Albert Docks, with tunicates also present below 2 m (Figure 6). All other groups increased over time, with macrophytes (initially chlorophytes, later rhodophytes) more abundant in shallower water, and other filter feeders (sponges and tunicates) more prevalent in deeper water. By 2012, most groups were present at all depths, maintaining similar patterns of relative abundance differences as described earlier. The presence of epibionts can obscure the visibility of mussels in photo-quadrats. As epibiont cover was greatest in 2012, it is possible that mussel % cover may have been slightly underestimated and the estimated 55-56% cover in Queens and Albert Docks could be viewed as a conservative estimate. Either way, the percentage cover of mussels in both docks remains high, suggesting that mussels are persisting in this novel ecosystem.

The starfish *Asterias rubens*, a key predator of *Mytilus* mussels, was first sighted in Albert Dock in 1995 (Fielding 1997). In February 2012, it was found in a single transect (4 quadrats in total, two at 3 m and two at 4 m). This transect exhibited significantly lower *Mytilus* cover (44 %) compared to the other two surveyed transects (PERMANOVA, P < 0.05), with the transect furthest from the starfish showing the highest cover (68 %). No *A. rubens* were observed in Queens Dock in 2012, and there were no reports of *A. rubens* in either dock in 2022.

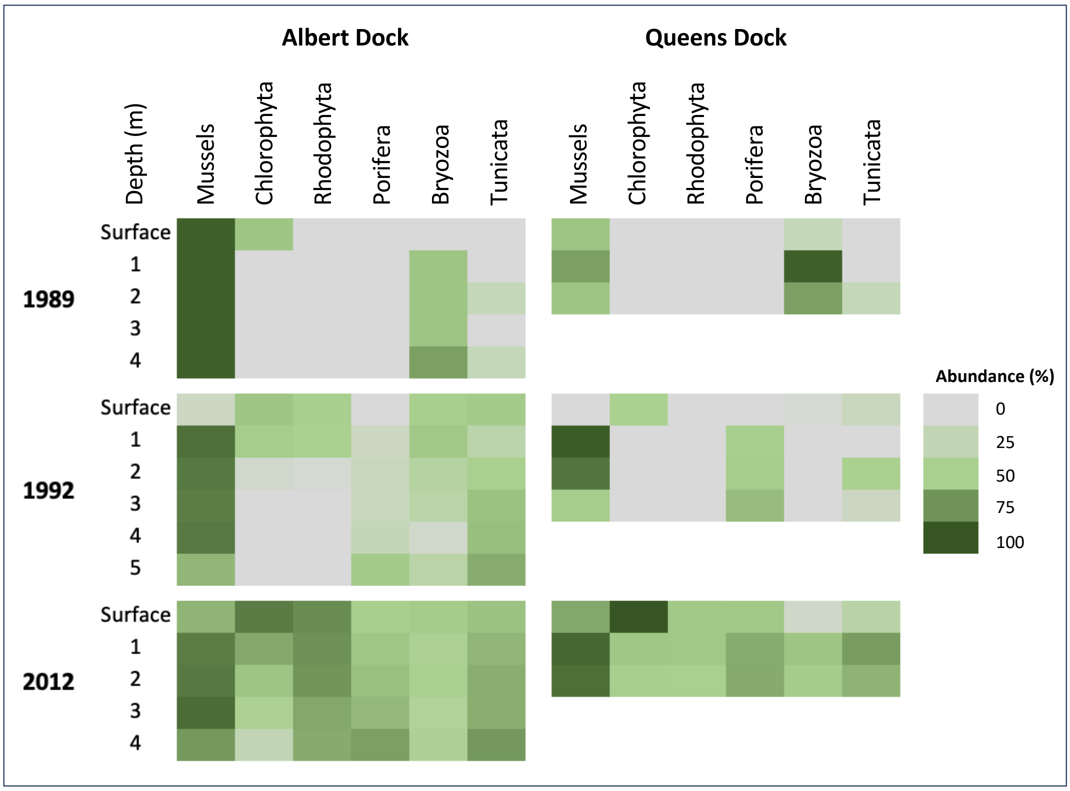

Figure 6. Heatmap showing the percentage cover of key taxonomic groups at different depths in Albert and Queens Docks Only data from summer 1989, 1992 and 2012 as they were the most complete (i.e., multiple depths were sampled in each year). Other data are available from different years/seasons/depth combinations (Allen 1992, Wilkinson 1995).

In 2012, destructive sampling of algae identified a total of 89 taxa (20 macrophytes and 69 diatoms) across Albert and Queens Docks (Table S3). Dinoflagellates and euglenoids were absent. The diatom community was diverse, encompassing both sessile and motile forms. Generally, the findings mirrored the photo-quadrat observations, with taxonomic richness within each group decreasing with depth (except for diatoms in Queens). The higher number of taxa observed in Albert (85) compared to Queens (56) is likely attributed to differences in sampling effort and not the added depth (only two taxa were unique to samples >2m in Albert: *Cyclotella kuetzingiana, Skeletonema costatum*), with more transects sampled in Albert.

Estimation of mussel clearance rates

Mussel clearance rate (CR) varied depending on location and depth (ANOVA, $F_{10,2999}$ = 67.57, $p < 0.001$) (Figure 7a). Even within Albert Dock, there were significant differences in individual clearance rates among sites and depths (Fig. 7a), with declines in CR with depth at Albert 2 and 3 but no clear pattern at Albert 1 and very low rates on the pontoon. In Queen's Dock, individual CR was consistent across all 3 sampled depths. Variation in CR_{INDIV} differed by up to ~3.65×, with minimum and max CR_{INDIV} ranging from as low as 0.51 L hr^{-1} on Albert Pontoon up to 1.86 L hr^{-1} at Albert 3 at 1 m depth.

Mussels occurred in different densities at different depths depending on location (ANOVA, $F_{10, 62}$ = 3.74, $p < 0.001$) resulting in CR_{PATCH} that differed in pattern to individual CR estimates (Figure 7b). Lowest mean CR_{PATCH} was estimated at Albert 2 at

4 m depth (18.9 L hr^{-1} 0.25 m^{-2}), and 5.2-fold higher at Albert 3 surface (98.7 L hr^{-1} 0.25 m^{-2}).

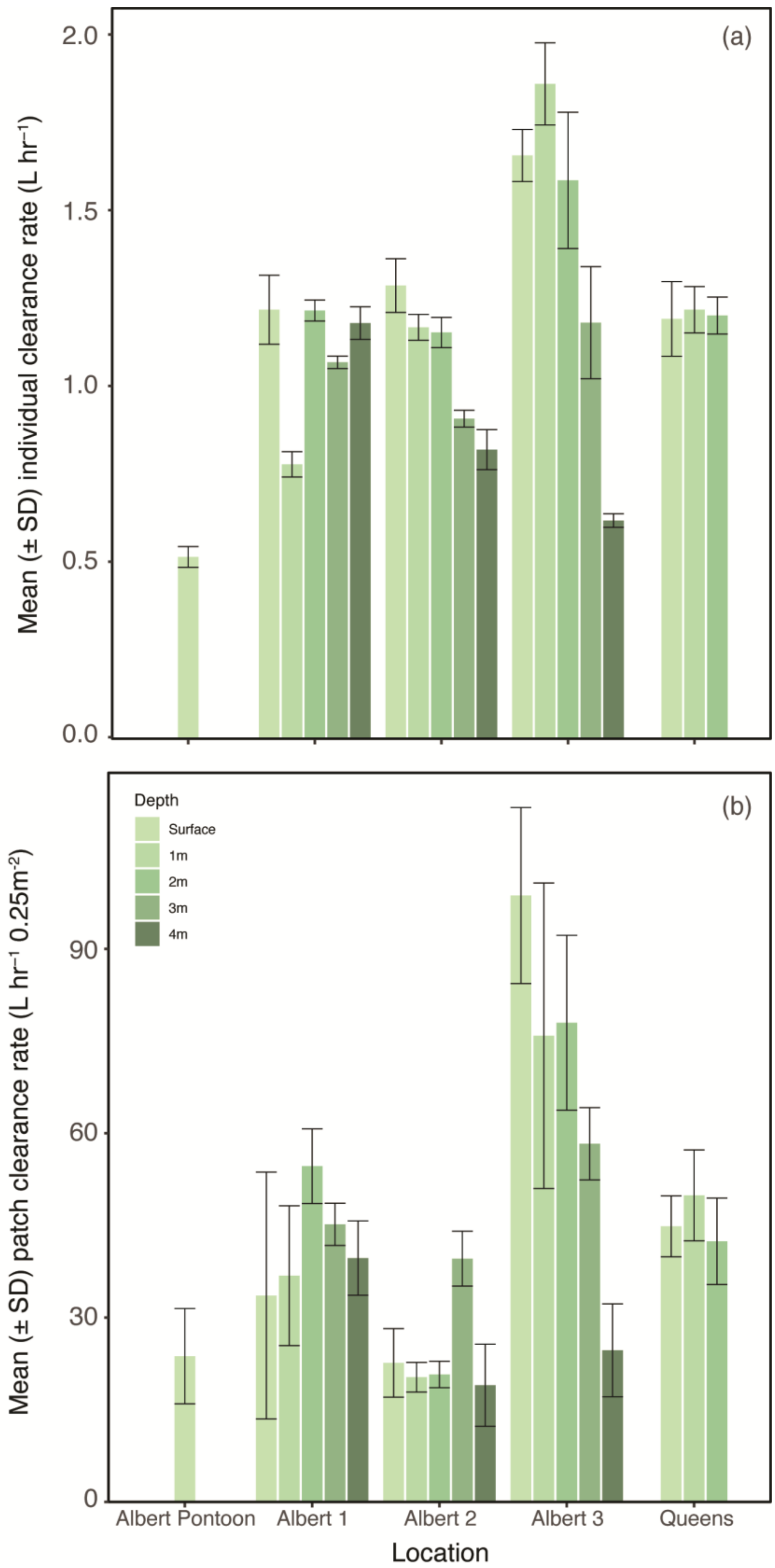

Figure 7. Mean clearance rate (± SD) of (a) individual mussels (L hr^{-1}), and (b) patch (L hr^{-1} m^2) in Albert and Queens Dock at 5 different water depths (Surface, 1 m, 2 m, 3 m and 4 m).

Discussion

The Liverpool Dock complex forms an urban novel ecosystem with 664 ha of built land, including 218 ha of continually submerged dock basin and over 11 km of seawall exposed to regular tides. This study spans approximately 40 years post the early 1980s restoration of Liverpool Docks. Following rapid ecological succession and water quality improvement, Albert and Queens Docks became dominated by mussels in the late 1980s. Despite seasonal and annual fluctuations, both docks stabilized environmentally by the mid-1990s. Sampling in 2012 and 2022 confirmed mussel dominance on dock walls. Since 2007, water clarity has been similar in both docks and consistently greater than the 2 m minimum standard clarity depth. Prior to that, clarity in Queens Dock was consistently lower than that in Albert Dock. A salinity drop occurred in both docks in 2022, likely from heavy July rains but there was evidence of recovery. Ensuring tidal gate seawater intake is crucial to balance salinity and discharge freshwater during Albert Dock gate closures on outgoing tides. While docks show stability in certain physico-chemical parameters (e.g., temperature, DO), managing the hydrological regime is crucial to maintain optimal salinity for mussel population persistence, ecosystem functioning, and service provision.

Following a natural settlement event in 1988, mussels colonized the dock walls and grew over time. Between 1989 and 1996, mussel populations exhibited a general increase in median mussel length and a consistent decrease in density. In 2012 and 2022, mussels continued to dominate the benthic assemblage, but the median shell length in both docks was smaller in 2022 than it was in 2012. Similarly, in 2012, in Queens dock, the median length was slightly lower than it was in 1996. This suggests either a major mortality event which killed off the larger, older mussels or a possible recruitment event in the preceding years. In the absence of major predators, *Mytilus edulis* can live for over 17-20 years on natural rocky shores in the UK (Seed 1969). While we do not know how old the mussels are in the Liverpool Docks, 37% of all mussels measured in August 2012 were >70 mm in length (in comparison to 5% that were <15 mm), suggesting an aging population. Our additional winter surveys in 2012 showed that not only was recruitment occurring between February and August, but that mussels were also growing in length (particularly the smaller individuals on the pontoons) during this time. Shell length, growth and lifespan all vary with environmental conditions (Kautsky 1982; Steffani and Branch, 2003). Given that the environmental conditions in the Liverpool docks are highly novel, making comparisons with natural ecosystems is a bit challenging.

The benthic assemblages associated with the mussels changed over time and patterns differed between the two docks. In 1989, the shells of the mussels predominantly hosted bryozoans and to a lesser extent, tunicates. The mussels at the surface in Albert Dock also supported green algae but Queens did not. By 1989, bryozoan cover had decreased in both docks allowing for the expansion of other taxa. Green algae and red algae were observed in the shallower depths in Queens and Albert Docks respectively, and sponges were observed in deeper water in both docks. By 2012, most groups were present at all depths, showing similar patterns as described above. The pattern of Queens supporting lower abundances number of species of algae continued throughout the survey period. This was evidenced both through the non-destructive photo-quadrat sampling (not identified to species level), and through the destructive hand-grab sampling of micro- and macro-algae (identified to species). Initially, the delayed arrival of both green and red algae in Queens Dock may be linked to the lower water clarity (and thus reduced light for photosynthesis) in Queens Dock. Light limitation is well known to have negative impacts on algal growth and functioning (Cloern 1999; Markager and Sand-Jensen 1992). Similarly, it could simply be due to greater influx of seawater into Albert Dock due to its proximity to the lock gate to the Mersey estuary. Queens Dock, by comparison is further away from a lock gate and thus may receive fewer propagules.

Red algae were slower to colonise both docks. This is perhaps not surprising as many red algae are classed as late successional species (Sousa 1979) and often take longer to colonise newly available substrata.

One of the most notable changes observed between the initial phase of research and the 2012 survey was the marked increase in red algae abundance. Red algae are generally considered indicators of good water quality (Sheath and Wehr, 2015), suggesting water quality in the docks has improved sufficiently that this species is present in much higher abundances. Though a small number of red algae species can actually be indicators of polluted waters (Sheath and Wehr, 2015) and as this study did not identify red algae to species level it is not possible to rule out this possibility. In addition to the increase in abundance, both red and green algae were present at greater depths. This suggests that light was able to penetrate deeper through the water, indicative of improved water clarity. This aligns with the fact that Albert Dock and adjacent Salthouse Dock were recently awarded a blue flag for water quality (Canal & River Trust, 2021, 2022).

Perennial algae species were absent in both 1992 and 2012. The 2012 surveys, conducted in February and August, missed the brown phase of the seasonal floristic cycle in the docks, characterized by dominance of brown macrophytes. The flora of the docks remains limited, comprising mainly ephemeral annual species, with perennial flora typical of the outer Mersey absent. Several factors, including high summer temperatures and inadequate water movement within the South Docks, inhibit the development of native canopy-forming species such as kelps and fucoids. In the mid-1990s, Wilkinson et al. (1996) identified the diatoms *Lycmophora* and *Melosira* as dominant taxa in the South Docks, with *Achnanthes* occurring sporadically in samples. *Achnanthes* has now become a persistent dominant taxon throughout the year. These algae not only play a crucial role in nutrient absorption, reducing the likelihood of unsightly or toxic algal blooms, but also contribute significantly to carbon assimilation (Thomas Kiran et al., 2015).

It is notable that the epifaunal communities associated with mussels in the dock system were dominated by filter feeders. Other filter feeding species may enhance community resilience and may also contribute to improving water quality. In 2012 there was an increase in the abundance of two key groups of filter feeders; sponges and tunicates. The insurance hypothesis proposes that other species might occupy the same niche after the failure of one species (Yachi & Loreau, 1999). Whilst sponges and tunicates are filter feeders which may maintain the water quality and clarity, they do not represent the same level of habitat provision as mussels (Bracewell et al., 2018), although, the shells of dead bivalves can provide important secondary substrata for attachment by other organisms (Tomatsuri and Kon 2017; Firth et al. 2021). Therefore, while sponges and tunicates may contribute significantly to maintaining water quality, they cannot fully replace the ecological role of mussels, highlighting the importance of mussel shells as secondary substrata for supporting diverse epibiotic communities.

Filtration rates of mussels varied significantly based on location, depth, and density (Figure 7a, b), exceeding 50 L hr-1 0.25 m^{-2} in several instances. Wilkinson et al. (1996) raised concerns about the long-term sustainability of mussel biofiltration due to limited recruitment in the mid-1990s. However, our recent findings indicate that mussels continue to play a role in maintaining water quality through biofiltration even after 30 years. Recent surveys also revealed that larvae readily recruit to newly available space on freshly deployed pontoons and areas disturbed by boat activity. Our assessment of filtration rates focused solely on mussel populations on dock walls. Future studies should adopt a more comprehensive approach and consider the relative sizes and densities of mussels, the surrounding environmental conditions, in addition to all filter-feeding organisms and novel substrates such as pontoons and other infrastructure (e.g. pilings and moorings) which are important substrata for filter-feeding organisms (Hughes et al., 2005; Layman et al., 2014; Mayer-Pinto et al., 2024). Our study highlights the critical role of mussels as ecosystem engineers in the

South Dock system, supporting other work suggesting the important role of bivalves in natural and degraded ecosystems (McFarland and Hare, 2018; Fariñas-Franco et al., 2023). The mussels act not only as habitat formers, supporting a dynamic epibiotic community that evolved over time, but also likely act as significant habitat modifiers through biofiltration.

Conclusions

Urban novel ecosystems can provide diverse ecosystem services that benefit economies and societies. The revitalization of disused docks in Liverpool, including structural restoration of surrounding buildings and rehabilitation of dock basin ecosystems, was pivotal in transforming a once-deprived area designated as an EU Objective 1 zone. By 1989, attractions at the culturally rich Albert Dock complex alone drew 3.5 million visitors, showcasing a blend of heritage preservation, waterfront attractiveness, and vibrant aquatic ecosystems (West, 2022).

This successful restoration contributed significantly to Liverpool being designated a UNESCO World Heritage Site (Liverpool Maritime Mercantile City) in 2004 and hosting the European Capital of Culture in 2008. These accolades boosted tourism and spurred investment in the city. However, the World Heritage status was rescinded in 2021 due to modernist development encroaching on the historic landscape, including proposed plans for a football stadium on a disused dock site.

Research increasingly demonstrates that urban regeneration projects improve mental and physical well-being by providing spaces for social integration and mental restoration, particularly benefiting communities of lower socioeconomic status (Baba et al., 2017; EEA, 2020; Teixeria and Fernandes, 2020; Ward Thompson et al., 2016). In our urbanizing world, these novel ecosystems should be integrated into management strategies to optimize their multifunctional benefits, enhancing connections between people and nature.

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Tables

Table 1. Summary of outputs from statistical analyses (2-Factor PERMANOVA) comparing physico-chemical parameters between docks (Albert, Queens) and among years.

Variable	Factor	F	P	Significance
Temperature	Dock	12.359	0.0002	**
	Year	4.1257	0.0001	**
	Do x Ye	0.99631	0.461	
Salinity	Dock	0.11079	0.7276	
	Year	9.0289	0.0001	**
	Do x Ye	0.29663	0.9743	
DO	Dock	3.9114	0.0515	
	Year	0.0674	0.0013	**
	Do x Ye	0.4996	0.1436	
Chlorophyll a	Dock	5.6541	0.0179	
	Year	0.9821	0.0377	*
	Do x Ye	0.7191	0.0048	**
Water clarity	Dock	79.41	0.0001	**
	Year	10.839	0.0001	**
	Do x Ye	5.7944	0.0001	**

Table 2. Summary of the minimum, maximum and mean values for each physico-chemical parameter measured at the surface or 1m above the bottom in Albert and

Queens Docks across the summer months (June-August) during the whole survey period (1988-2022).

Parameter	Depth	Depth	Albert	Queens
Temperature (℃)	Surface	Min	14.5	14.8
		Max	22.8	23.8
		Mean	18.5	19
	Bottom	Min	13.2	14.2
		Max	20.9	23
		Mean	17.5	18.6
Salinity	Surface	Min	10.2	19.4
		Max	28.6	28.7
		Mean	24.5	25.5
	Bottom	Min	19.1	21.9
		Max	29.9	30.3
		Mean	25.8	25.7
Dissolved oxygen (mg/L)	Surface	Min	5.44	4.93
		Max	16.8	12
		Mean	8.4	8
	Bottom	Min	0.5	1.4
		Max	10.9	12.6
		Mean	5.2	6.6
Chlorophyll a (mg/L)	Surface	Min	0.8	1
		Max	43.5	60.4
		Mean	9.6	12.9
Secchi depth (m)	N/A	Min	1	0.7
		Max	5.4	4.1
		Mean	3.2	2.3