CORA Cork Open Research Archive
Cartlann Taighde Oscailte Chorcaí

Title	Ecosystem engineers enhance the multifunctionality of an urban novel ecosystem: Population persistence and ecosystem resilience since the 1980s
Authors	Firth, Louise B.;Forbes, Anastasia;Knights, Antony M.;O'Shaughnessy, Kathryn A.;Mahmood-Brown, Wahaj;Struthers, Lewis;Hawcutt, Ellie;Bohn, Katrin;Sayer, Martin D. J.;Quinn, James;Allen, Jan;Dürr, Simone;Guerra, Maria Teresa;Leeper, Alexandra;Mieszkowska, Nova;Reid, Geraldine;Wilkinson, Stephen;Williams, Adrian E.;Hawkins, Stephen J.
Publication date	2024-09-06
Original Citation	Firth, L. B., Forbes, A., Knights, A. M., O'Shaughnessy, K. A., Mahmood-Brown, W., Struthers, L., Hawcutt, E., Bohn, K., Sayer, M., Quinn, J., Allen, J., Dürr, S.,Guerra, M. T., Leeper, A., Mieszkowska, N., Reid, G., Wilkinson, S., Williams, A. E. and Hawkins, S. J. (2024) 'Ecosystem engineers enhance the multifunctionality of an urban novel ecosystem: Population persistence and ecosystem resilience since the 1980s', Science of the Total Environment, 952, 175675 (14pp). https://doi.org/10.1016/j.scitotenv.2024.175675
Type of publication	Article (peer-reviewed)
Link to publisher's version	10.1016/j.scitotenv.2024.175675
Rights	© 2024 Elsevier B.V. All rights are reserved, including those for text and data mining, AI training, and similar technologies. This manuscript version is made available under the CC BY-NC-ND 4.0 license - https://creativecommons.org/licenses/by-nc-nd/4.0/
Download date	2026-11-16 05:56:07
Item downloaded from	https://hdl.handle.net/10468/16509



University College Cork, Ireland
Coláiste na hOllscoile Corcaigh

Pre-proof of Firth et al. (2024). Ecosystem engineers enhance the multifunctionality of an urban novel ecosystem: population persistence and ecosystem resilience since the 1980s. *Science of the Total Environment.* https://doi.org/10.1016/j.scitotenv.2024.175675

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

Louise B. Firth[1,2,3,4], Anastasia Forbes[1], Antony M. Knights[1,4], Kathryn A. O'Shaughnessy[5,6], Wahaj Mahmood-Brown[1], Lewis Struthers[7], Ellie Hawcutt[1], Katrin Bohn[3,4,8,9], Martin Sayer[10,11], James Quinn[12], Jan Allen[13], Simone Dürr[14], Maria Teresa Guerra[15], Alexandra Leeper[3,16], Nova Mieszkowska[7,17], Geraldine Reid[18], Stephen Wilkinson[13,19,20], Adrian E. Williams[5], Stephen J. Hawkins[1,3,,8,13,16,19]

[1] School of Biological and Marine Sciences, University of Plymouth, Plymouth, PL4 8AA, United Kingdom

[2] Zoology Department, National University of Ireland Galway, Galway, Ireland

[3] School of Ocean Sciences, Bangor University, Bangor, United Kingdom

[4] Current address: School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland

[5] APEM Ltd, Stockport, United Kingdom

[6] Current address: Dauphin Island Sea Lab, Dauphin Island, Alabama, United States of America

[7] School of Environmental Sciences, University of Liverpool, L69 3BX, United Kingdom

[8] Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, Southampton, SO14 3ZH, United Kingdom

[9] Current address: Natural England, Nottingham, NG2 4LA, United Kingdom

[10] NERC National Facility for Scientific Diving, Dunstaffnage Marine Laboratories, Oban PA37 1QA, United Kingdom

[11] Current: Tritonia Scientific Ltd., Dunstaffnage Marine Laboratories, Oban PA37 1QA, United Kingdom

[12] School of Geography and Environmental Sciences, University of Plymouth, Plymouth, Plymouth, PL4 8AA, United Kingdom

[13] Department of Environmental and Evolutionary Biology, University of Liverpool, L69 3BX, United Kingdom

[14] School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, L3 3AF, United Kingdom

[15] Department of Biological and Environmental Science and Technologies (DiSTeBA), Lecce, Italy

[16] Department of international affairs, Iceland Ocean Cluster, Reykjavik 101, Iceland.

[17] The Marine Biological Association of the UK, Plymouth, PL1 2PB, United Kingdom

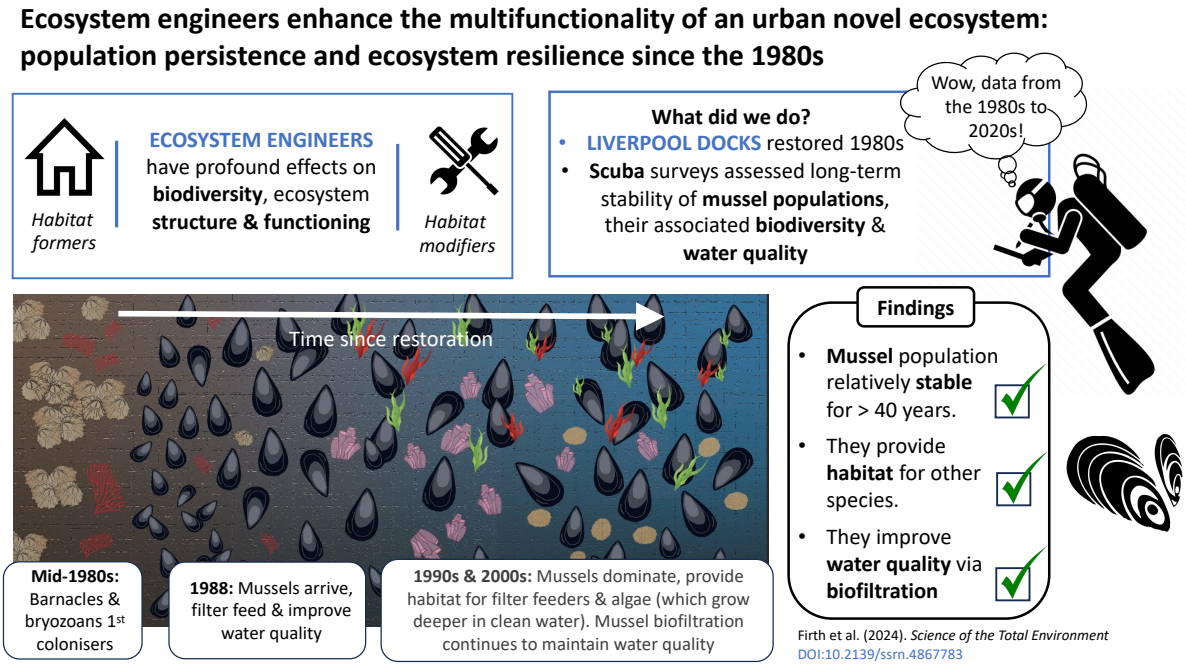
[18] Botany, World Museum, National Museums Liverpool, L3 8EN, United Kingdom

[19] Port Erin Marine Laboratory, University of Liverpool, Port Erin, Isle of Man, IH49 6JA

[20] Current address: Joint Nature Conservation Committee, Peterborough, PE1 1JY, United Kingdom

Pre-proof of Firth et al. (2024). Ecosystem engineers enhance the multifunctionality of an urban novel ecosystem: population persistence and ecosystem resilience since the 1980s. *Science of the Total Environment.* https://doi.org/10.1016/j.scitotenv.2024.175675

Graphical Abstract



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

153 waterfront buildings and dock warehouses (Figure 1b). The health and attractiveness
154 of the aquatic ecosystems in the dock basins were crucial to the success of the
155 surrounding restored and repurposed warehouse buildings. Initially, however, the
156 water quality was very poor. These initiatives were particularly challenging given that
157 the Mersey was one of the most polluted catchments and estuaries in the UK and
158 Europe, necessitating a massive clean-up campaign from the 1980s onwards (see
159 Hawkins et al., 2020 for review).

160

161 Early initiatives included mussel aquaculture in Sandon Dock (Hawkins et al., 1992a,
162 b). The top-down biofiltration by mussels on ropes and dock walls, combined with
163 bottom-up artificial mixing via an air lift pump, significantly improved water quality
164 (Russell et al., 1983). These lessons were then applied to managing the poor water
165 quality in the South Docks complex, centred around the iconic Albert Dock, which
166 underwent redevelopment including dredging and water replacement between 1981
167 and 1985. A critical factor in the rapid water quality improvement of the South Docks
168 was the natural colonization of dense mussel (*Mytilus* spp.) populations on the dock
169 walls, acting as biofilters and secondary habitat for a wide range of species (Figure
170 1c,d, Allen et al., 1992; Allen and Hawkins, 1993; Wilkinson et al., 1996). Revisiting this
171 novel ecosystem provides invaluable insights into the long-term performance of
172 rehabilitation projects, particularly highlighting the role of top-down control through
173 bivalve biofiltration and the manipulation of bottom-up processes through mixing.
174

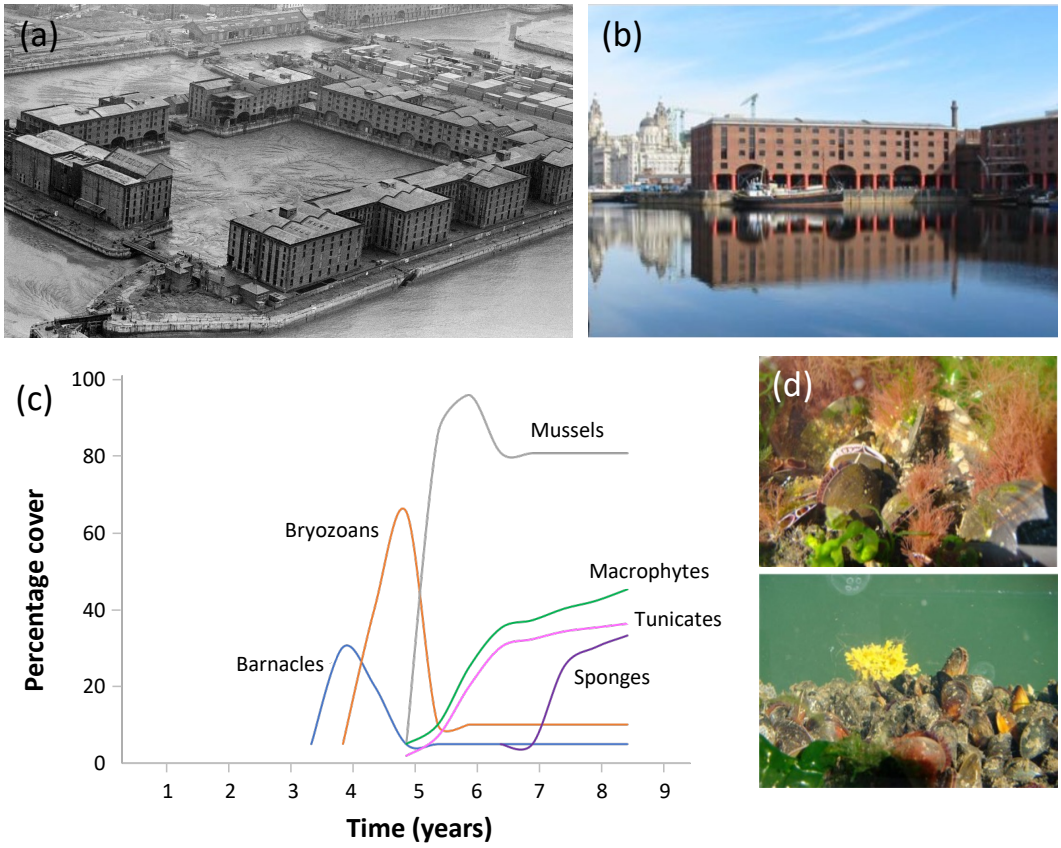


Figure 1. The Liverpool Docks: an urban novel ecosystem. (a) The Albert Dock full of silt prior to dredging and restoration work in 1980. (b) The Albert Dock in 2012 – part of the then Liverpool Maritime Mercantile City UNESCO World Heritage Site (lost UNESCO status in 2021). (c) Schematic diagram showing 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.

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

195 (1) Quantify the extent of novel habitats and built land.
196 (2) Describe changes in the physico-chemical parameters of the water.
197 (3) Quantify the changes in cover and population structure of mussels (*Mytilus*
198 spp.), the key ecosystem engineers in this system.
199 (4) Chart long-term successional changes in the associated benthic assemblage.
200 (5) Estimate contemporary biofiltration rates by mussels.

201

202 **Materials and Methods**

203 ***Study system: the Liverpool South Dock Complex***

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

209

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

310 from the summer months (June to August) of each year were included due to data
311 availability. Efforts primarily focused on periods when water quality issues like anoxia
312 and algal blooms—often linked to water column stratification—were more likely to
313 occur. Differences in physico-chemical variables were tested using Two-Factor
314 PERMANOVA with Factors Dock (Albert, Queens; fixed factor) and Year (various, fixed,
315 orthogonal). To restrict comparisons to overall trends, depth was not included as a
316 factor in the statistical analysis but is maintained in the figures. Univariate
317 PERMANOVA was chosen for univariate analyses because it allows for two-factor
318 designs, considers an interaction term and does not assume a normal distribution of
319 errors. The tests were run on Euclidean distances matrices with 9999 permutations
320 (Anderson, 2001).
321
322 ***Mussel population density and structure in Queens and Albert Docks***
323 Historical data spanning 1989 to 1996 were gathered from a variety of published and
324 unpublished sources, while re-surveys were conducted in 2012 and 2022 (see Table
325 S1 for data collection details across years and docks).
326
327 Except for 2022, mussel population density and structure data were collected using
328 identical methodology. For surveys conducted between 1989-1996 and 2012 SCUBA
329 divers scraped all mussels within 0.25 m × 0.25 m quadrats (3-5 replicates) into net
330 bags (1 mm mesh size) along at least two vertical transects per dock. Due to
331 restrictions on SCUBA diving in the docks, in July 2022, mussels were scraped from
332 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.

399 CR_{INDIV} data were then scaled-up to a 'patch' estimate, coupling individual CR with
400 survey estimates of mean mussel density per m^2 (D) as follows:
401 CR_{PATCH} (l h^{-1} m^{-2}) = $CR_{INDIV} \times D$ [2]
402 Variation in CR_{PATCH} was also estimated by as mean D ± the standard deviation in
403 density among quadrats. We tested for differences in CR_{INDIV} among locations and
404 sampling depth using two-factor analysis of variance performed in R (R Core Team,
405 2024).
406
407
408
409
410 **Results**
411 ***Extent of novel habitats and built land in the South Dock complex***
412 The construction of the Liverpool Dock complex on the east bank of the Mersey
413 (spanning from Crosby Beach in the north to the infilled Herculaneum Dock in the
414 south) resulted in the development of 664 ha of new land. This includes 218 ha of
415 continuously submerged dock basins and over 11 km of seawalls beyond the docks
416 exposed to regular tidal cycles (Figure 2). Specifically, the South Docks alone account
417 for 136 ha of constructed land, featuring 28.2 ha of dock basins and 3.2 ha of newly
418 submerged seawalls within the docks. Additionally, the installation of floating
419 pontoons in some docks has introduced an extra 0.4 ha of new floating habitat (Table
420 S2). The variations in depth, surface area, proximity to Mersey inflows, and the recent
421 connection to the Leeds Liverpool Canal in 2009 have created a mosaic of similar yet

422 slightly distinct standing water environments that support diverse biological
423 communities.
424
425 ***Physico-chemical parameters***
426 All physico-chemical variables differed significantly over time but only some differed
427 between docks (Table 1). While there was a significant main effect of Year,
428 temperature fluctuated over time and no clear trends or patterns emerged (Figure
429 3a). Notably, the warming trends observed in the waters surrounding the British Isles
430 post-1988 were not evident within the docks. Overall, temperature was significantly
431 higher in Queens Dock (average 18.8°C) compared to Albert Dock (18.0°C). Being
432 deeper than Queens Dock (<4 m), Albert Dock (<6 m) is more prone to natural thermal
433 stratification (Figure 3a, Table 1). From 1991 onwards, Albert Dock was artificially
434 mixed in summer using an airlift device, which mitigated stratification. In 1994,
435 operational issues with the device led to stratification (Wanstall, 1997). In recent
436 years, the device has not been used and was removed in 2022 (A. Goodey, Canals and
437 Rivers Trust, pers. comm.). Summer surface temperatures consistently exceeded
438 bottom temperatures in Albert Dock, with wider surface standard errors indicating
439 occasional stratification. Conversely, differences between surface and bottom
440 temperatures were generally smaller in Queens Dock, reflecting its shallower, more
441 open nature conducive to wind mixing. In 2022, surface temperatures in Queens Dock
442 were slightly lower than bottom temperatures, indicating cooler freshwater resting
443 above slightly warmer saline water (as evidenced in salinity differences, Figure 3b).
444

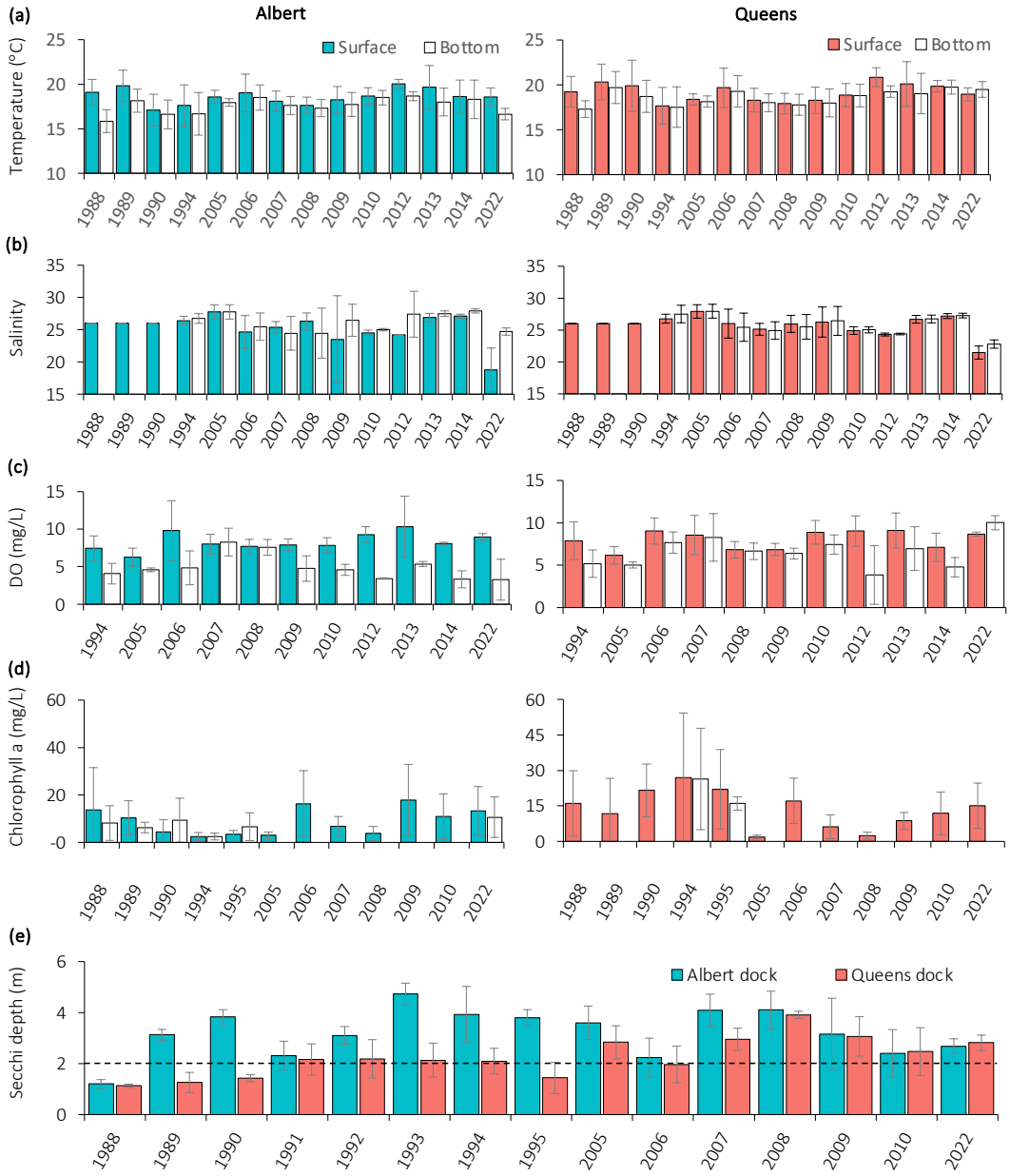


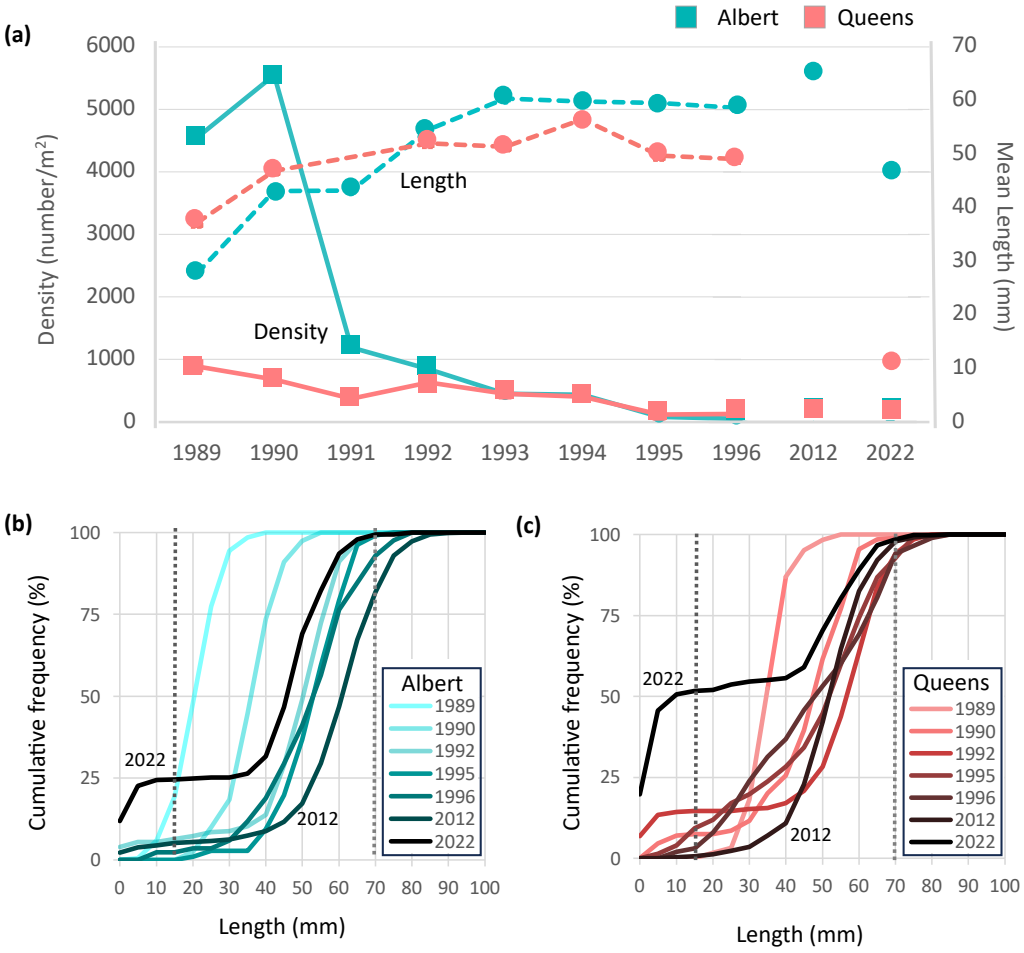
Figure 3. Variation in physico-chemical parameters in the summer months (June-August) in Albert Dock (blue) and Queens Dock (pink) between 1988 and 2022 (mean values ± S.E.). (a) temperature (°C); (b) salinity; (c) dissolved oxygen (DO, mg/L); (d) chlorophyll a (mg/L) (e); and water clarity depth (m). 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

452 on data sources. Not all parameters were measured in all years. Note that salinity for
453 1998-1990 was simply reported as 24-28 (Allen, 1992).
454
455 There was a significant main effect of Year on salinity (Table 1). In all years sampled
456 average summer salinity was consistently above 24 in both docks. In 2022, there was
457 a significant reduction in salinity (PERMANOVA, post hoc comparisons) and this was
458 observed in both Albert and Queens Docks. In Albert Dock, surface salinities
459 consistently remained below 22, reaching a low of 11 in July due to heavy rainfall and
460 runoff. Slightly higher salinities (17.6 and 21.4) were observed during the two
461 sampling events in August, suggesting possible recovery. A similar albeit less
462 pronounced decrease was noted in Queens Dock (consistently below 23, with a low of
463 19.4), suggesting that the closer proximity of Albert Dock to the freshwater input of
464 the Leeds-Liverpool Canal may be a factor driving the lower salinities observed.
465
466 There was a significant main effect of Year for dissolved oxygen and significant
467 interaction between Dock and Year for Chlorophyll a (Table 1). Typically, dissolved
468 oxygen levels were higher at the surface (always above 5 mg/L) than at the bottom
469 (often below 5 mg/L) across most years, but no other trends were obvious (Figure 3c).
470 No discernible trends were evident for Chlorophyll a (Figure 3d).
471
472 There was a significant interaction between Dock and Year for water clarity (Table 1).
473 Initially, in 1988, water clarity was similar in Albert and Queens Docks (~1.1 m), falling
474 below the minimum 2 m clarity standard. Water clarity in Albert Dock was significantly

475 deeper than Queens Dock for seven of the fifteen survey years (PERMANOVA, post
476 hoc comparisons: 1989, 1990, 1992, 1993, 1994, 1995, 2007). In Albert Dock, the only
477 clear temporal trend was that water clarity was significantly shallower in 1988
478 compared to all other years. From 1989 onwards, mean water clarity in Albert Dock
479 consistently exceeded 2.2 m, averaging 3.2 m annually. Conversely, water clarity in
480 Queens Dock remained consistently shallower than in Albert Dock during the early
481 years (often around or below 2 m until 1995; PERMANOVA, post hoc comparisons).
482 From 2008 onwards, water clarity depths increased (>2 m) and became more similar
483 between both docks and years, possibly due to increased boat traffic and sediment
484 disturbance following the Leeds-Liverpool Canal connection.
485
486 ***Mussel population structure and growth in Queens and Albert Docks***
487 Natural recruitment of mussels on the walls of both Albert and Queens Docks began
488 in 1988, four years after the dock-gates were reinstated and water retention began.
489 Initially, Albert Dock experienced very high densities (>4000/m^2 in both 1989 and
490 1990) due to a substantial recruitment event in summer/autumn 1988, likely
491 originating from the Mersey. In contrast, Queens Dock had lower densities
492 (<1000/m^2), possibly indicating a different route of recruitment or a lack of water flow
493 between Albert Dock (which is closer to the lock gate) and Queens Dock. Albert Dock's
494 mussel densities declined sharply over a 2-year period to around 1200/m^2 by 1991,
495 followed by a gradual decrease until stabilizing in the mid-1990s. Since 1995, densities
496 have fluctuated between a low of 53/m^2 in 1996 and a high of 224/m^2 in 2012. In
497 Queens Dock, densities were consistently lower than Albert's in the early years

498 (always below 1000/m^2). From 1992 onwards, densities have been similar, varying
499 between a low of 120/m^2 in 1995 and a peak of 350/m^2 in 2012.
500
501 Between 1989 and 1992/1993, the mean length of mussels in both docks increased
502 (Figure 4a), stabilizing around 50-60 mm. Initially, mussels were smaller in Albert Dock,
503 likely due to intense intraspecific competition. However, since 1992, they have
504 consistently been larger than those in Queens Dock. By 2022, both docks experienced
505 a significant decline in mean mussel length: Queens Dock decreased from 48 mm in
506 2012 to 10 mm in 2022, while Albert Dock dropped from 66 mm in 2012 to 47 mm in
507 2022.
508
509 The mussel population structure in both Albert and Queens Docks evolved over time.
510 Albert Dock underwent a rapid shift from a size structure dominated by recruits (<20
511 mm length) to larger mussels between 1989 and 1992 (Figure 4b, K-S Tests, $P < 0.05$),
512 driven by the initial massive colonizing cohort. From 1992 to 2012, although the
513 median size continued to increase (not significant, all K-S Tests, $P > 0.01$), indicating
514 sustained growth of the initial cohort. However, by 2022, the median size had
515 significantly decreased (~47 mm) compared to 2012 (~62 mm) (K-S Test, $P < 0.05$).
516
517 Queens Dock exhibited a different pattern (Figure 4c). Recruitment was slower
518 initially, but following a strong event in 1992, the population remained relatively
519 stable from 1992 to 1996. By 2012, the population structure had reverted to earlier
520 patterns, indicating possible recruitment events in the interim. Like Albert Dock, in

521 2022, the median size was significantly (K-S Test, $P < 0.05$) smaller (~10 mm) than in
522 2012 (~53 mm).
523



524

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

532

533 Surveys in 2012 indicated that mussel recruitment was observed at all depths in Albert
534 Dock, with the highest recruitment found at 3 to 4 m depth and the lowest near the
535 surface, possibly due to mortality linked to fluctuating water levels (Figure 5a). Median
536 mussel size showed a slight tendency to decrease with depth in both docks (Figure
537 5a).

538

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

545

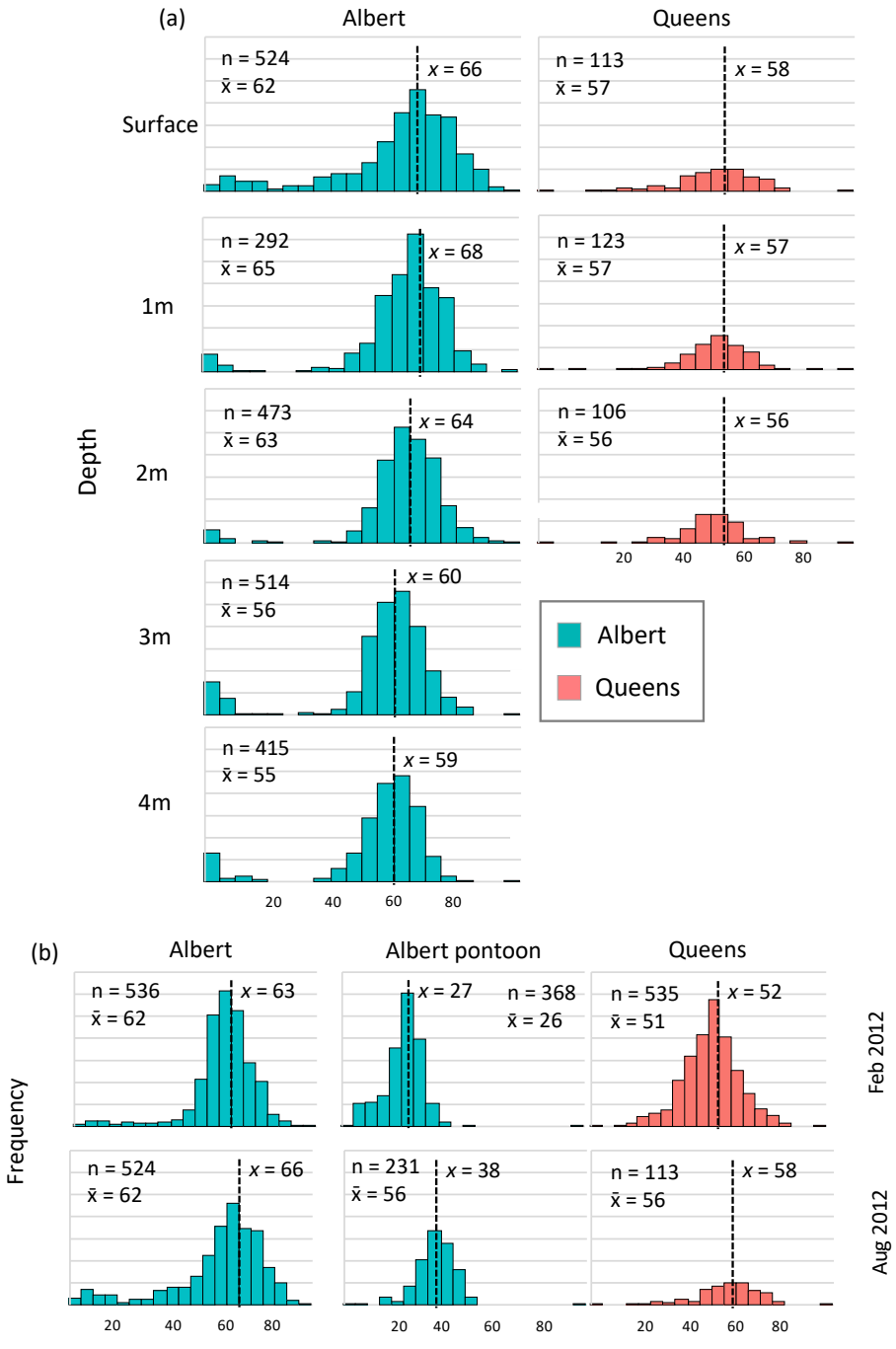


Figure 5. Length frequency histograms of *Mytilus* spp. populations in Albert and Queens Docks; (a) Depth gradient in 2012 and (b) Six months of mussel growth at the surface and on the pontoons between February and August 2012. Blue = Albert; pink = Queens.

551

552 ***Benthic assemblage associated with mussels in Albert and Queens Docks***

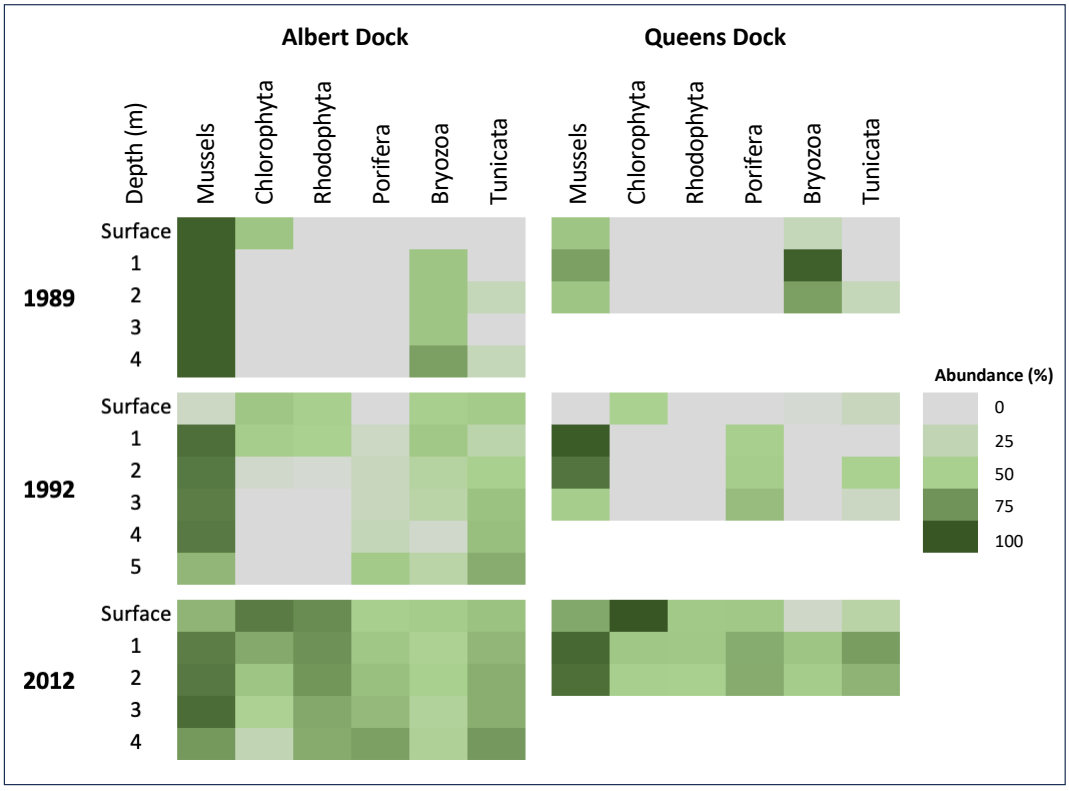
553 Mussel percentage cover in both docks typically showed lower values at the surface,
554 likely due to fluctuating water levels, and at the dock floor across all sampled years
555 (Figure 6). In Albert Dock, mussel cover fluctuated widely over time, peaking at around
556 75 % in 1989 and dropping to a low of 19 % in 1995 (Fielding, 1995, not shown in Figure
557 6). By 2012, mussel cover had rebounded to 56 % in Queens Dock and 55 % in Albert
558 Dock (PERMANOVA, $P > 0.05$).

559

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

572

573 The starfish *Asterias rubens*, a key predator of *Mytilus* mussels, was first sighted in
574 Albert Dock in 1995 (Fielding 1997). In February 2012, it was found in a single transect
575 (4 quadrats in total, two at 3 m and two at 4 m). This transect exhibited significantly
576 lower *Mytilus* cover (44 %) compared to the other two surveyed transects
577 (PERMANOVA, $P < 0.05$), with the transect furthest from the starfish showing the
578 highest cover (68 %). No *A. rubens* were observed in Queens Dock in 2012, and there
579 were no reports of *A. rubens* in either dock in 2022.
580

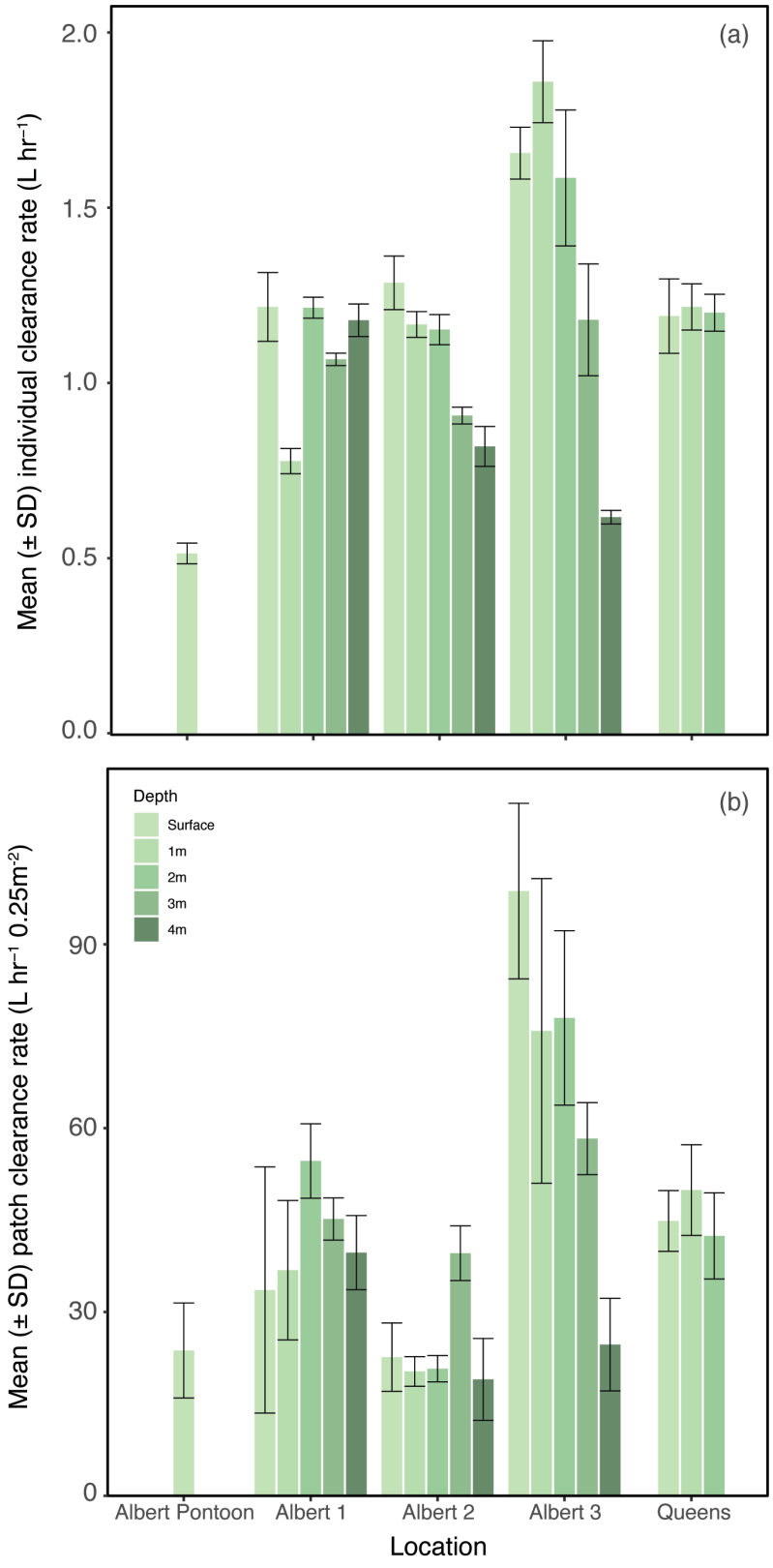


581

582 Figure 6. Heatmap showing the percentage cover of key taxonomic groups at different
583 depths in Albert and Queens Docks Only data from summer 1989, 1992 and 2012 as
584 they were the most complete (i.e., multiple depths were sampled in each year). Other

585 data are available from different years/seasons/depth combinations (Allen 1992,
586 Wilkinson 1995).
587
588 In 2012, destructive sampling of algae identified a total of 89 taxa (20 macrophytes
589 and 69 diatoms) across Albert and Queens Docks (Table S3). Dinoflagellates and
590 euglenoids were absent. The diatom community was diverse, encompassing both
591 sessile and motile forms. Generally, the findings mirrored the photo-quadrat
592 observations, with taxonomic richness within each group decreasing with depth
593 (except for diatoms in Queens). The higher number of taxa observed in Albert (85)
594 compared to Queens (56) is likely attributed to differences in sampling effort and not
595 the added depth (only two taxa were unique to samples >2m in Albert: *Cyclotella*
596 *kuetzingiana, Skeletonema costatum*), with more transects sampled in Albert.
597
598 ***Estimation of mussel clearance rates***
599 Mussel clearance rate (CR) varied depending on location and depth (ANOVA, $F_{10,2999}$ =
600 67.57, $p < 0.001$) (Figure 7a). Even within Albert Dock, there were significant
601 differences in individual clearance rates among sites and depths (Fig. 7a), with
602 declines in CR with depth at Albert 2 and 3 but no clear pattern at Albert 1 and very
603 low rates on the pontoon. In Queen's Dock, individual CR was consistent across all 3
604 sampled depths. Variation in CR_{INDIV} differed by up to ~3.65×, with minimum and max
605 CR_{INDIV} ranging from as low as 0.51 L hr^{-1} on Albert Pontoon up to 1.86 L hr^{-1} at Albert
606 3 at 1 m depth.
607

608 Mussels occurred in different densities at different depths depending on location
609 (ANOVA, $F_{10, 62}$ = 3.74, p < 0.001) resulting in CR_{PATCH} that differed in pattern to
610 individual CR estimates (Figure 7b). Lowest mean CR_{PATCH} was estimated at Albert 2 at
611 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
612 m^{-2}).
613


(a)
Mean (± SD) individual clearance rate (L hr⁻¹)
2.0
1.5
1.0
0.5
0.0
(b)
Depth
Surface
1m
2m
3m
4m
Mean (± SD) patch clearance rate (L hr⁻¹ 0.25m⁻²)
90
60
30
0
Albert Pontoon
Albert 1
Albert 2
Albert 3
Queens
Location

614

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

618

619 **Discussion**

620 The Liverpool Dock complex forms an urban novel ecosystem with 664 ha of built land,
621 including 218 ha of continually submerged dock basin and over 11 km of seawall
622 exposed to regular tides. This study spans approximately 40 years post the early 1980s
623 restoration of Liverpool Docks. Following rapid ecological succession and water quality
624 improvement, Albert and Queens Docks became dominated by mussels in the late
625 1980s. Despite seasonal and annual fluctuations, both docks stabilized
626 environmentally by the mid-1990s. Sampling in 2012 and 2022 confirmed mussel
627 dominance on dock walls. Since 2007, water clarity has been similar in both docks and
628 consistently greater than the 2 m minimum standard clarity depth. Prior to that, clarity
629 in Queens Dock was consistently lower than that in Albert Dock. A salinity drop
630 occurred in both docks in 2022, likely from heavy July rains but there was evidence of
631 recovery. Ensuring tidal gate seawater intake is crucial to balance salinity and
632 discharge freshwater during Albert Dock gate closures on outgoing tides. While docks
633 show stability in certain physico-chemical parameters (e.g., temperature, DO),
634 managing the hydrological regime is crucial to maintain optimal salinity for mussel
635 population persistence, ecosystem functioning, and service provision.

636

637 Following a natural settlement event in 1988, mussels colonized the dock walls and
638 grew over time. Between 1989 and 1996, mussel populations exhibited a general
639 increase in median mussel length and a consistent decrease in density. In 2012 and
640 2022, mussels continued to dominate the benthic assemblage, but the median shell
641 length in both docks was smaller in 2022 than it was in 2012. Similarly, in 2012, in
642 Queens dock, the median length was slightly lower than it was in 1996. This suggests
643 either a major mortality event which killed off the larger, older mussels or a possible
644 recruitment event in the preceding years. In the absence of major predators, *Mytilus*
645 *edulis* can live for over 17-20 years on natural rocky shores in the UK (Seed 1969).
646 While we do not know how old the mussels are in the Liverpool Docks, 37% of all
647 mussels measured in August 2012 were >70 mm in length (in comparison to 5% that
648 were <15 mm), suggesting an aging population. Our additional winter surveys in 2012
649 showed that not only was recruitment occurring between February and August, but
650 that mussels were also growing in length (particularly the smaller individuals on the
651 pontoons) during this time. Shell length, growth and lifespan all vary with
652 environmental conditions (Kautsky 1982; Steffani and Branch, 2003). Given that the
653 environmental conditions in the Liverpool docks are highly novel, making comparisons
654 with natural ecosystems is a bit challenging.
655
656 The benthic assemblages associated with the mussels changed over time and patterns
657 differed between the two docks. In 1989, the shells of the mussels predominantly
658 hosted bryozoans and to a lesser extent, tunicates. The mussels at the surface in
659 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

683 present in much higher abundances. Though a small number of red algae species can
684 actually be indicators of polluted waters (Sheath and Wehr, 2015) and as this study
685 did not identify red algae to species level it is not possible to rule out this possibility.
686 In addition to the increase in abundance, both red and green algae were present at
687 greater depths. This suggests that light was able to penetrate deeper through the
688 water, indicative of improved water clarity. This aligns with the fact that Albert Dock
689 and adjacent Salthouse Dock were recently awarded a blue flag for water quality
690 (Canal & River Trust, 2021, 2022).
691
692 Perennial algae species were absent in both 1992 and 2012. The 2012 surveys,
693 conducted in February and August, missed the brown phase of the seasonal floristic
694 cycle in the docks, characterized by dominance of brown macrophytes. The flora of
695 the docks remains limited, comprising mainly ephemeral annual species, with
696 perennial flora typical of the outer Mersey absent. Several factors, including high
697 summer temperatures and inadequate water movement within the South Docks,
698 inhibit the development of native canopy-forming species such as kelps and fucoids.
699 In the mid-1990s, Wilkinson et al. (1996) identified the diatoms *Lycmophora* and
700 *Melosira* as dominant taxa in the South Docks, with *Achnanthes* occurring sporadically
701 in samples. *Achnanthes* has now become a persistent dominant taxon throughout the
702 year. These algae not only play a crucial role in nutrient absorption, reducing the
703 likelihood of unsightly or toxic algal blooms, but also contribute significantly to carbon
704 assimilation (Thomas Kiran et al., 2015).
705

706 It is notable that the epifaunal communities associated with mussels in the dock
707 system were dominated by filter feeders. Other filter feeding species may enhance
708 community resilience and may also contribute to improving water quality. In 2012
709 there was an increase in the abundance of two key groups of filter feeders; sponges
710 and tunicates. The insurance hypothesis proposes that other species might occupy the
711 same niche after the failure of one species (Yachi & Loreau, 1999). Whilst sponges
712 and tunicates are filter feeders which may maintain the water quality and clarity, they
713 do not represent the same level of habitat provision as mussels (Bracewell et al.,
714 2018), although, the shells of dead bivalves can provide important secondary
715 substrata for attachment by other organisms (Tomatsuri and Kon 2017; Firth et al.
716 2021). Therefore, while sponges and tunicates may contribute significantly to
717 maintaining water quality, they cannot fully replace the ecological role of mussels,
718 highlighting the importance of mussel shells as secondary substrata for supporting
719 diverse epibiotic communities.
720
721 Filtration rates of mussels varied significantly based on location, depth, and density
722 (Figure 7a, b), exceeding 50 L hr-1 0.25 m^{-2} in several instances. Wilkinson et al. (1996)
723 raised concerns about the long-term sustainability of mussel biofiltration due to
724 limited recruitment in the mid-1990s. However, our recent findings indicate that
725 mussels continue to play a role in maintaining water quality through biofiltration even
726 after 30 years. Recent surveys also revealed that larvae readily recruit to newly
727 available space on freshly deployed pontoons and areas disturbed by boat activity.
728 Our assessment of filtration rates focused solely on mussel populations on dock walls.

729 Future studies should adopt a more comprehensive approach and consider the
730 relative sizes and densities of mussels, the surrounding environmental conditions, in
731 addition to all filter-feeding organisms and novel substrates such as pontoons and
732 other infrastructure (e.g. pilings and moorings) which are important substrata for
733 filter-feeding organisms (Hughes et al., 2005; Layman et al., 2014; Mayer-Pinto et al.,
734 2024). Our study highlights the critical role of mussels as ecosystem engineers in the
735 South Dock system, supporting other work suggesting the important role of bivalves
736 in natural and degraded ecosystems (McFarland and Hare, 2018; Fariñas-Franco et al.,
737 2023). The mussels act not only as habitat formers, supporting a dynamic epibiotic
738 community that evolved over time, but also likely act as significant habitat modifiers
739 through biofiltration.
740

741 **Conclusions**

742 Urban novel ecosystems can provide diverse ecosystem services that benefit
743 economies and societies. The revitalization of disused docks in Liverpool, including
744 structural restoration of surrounding buildings and rehabilitation of dock basin
745 ecosystems, was pivotal in transforming a once-deprived area designated as an EU
746 Objective 1 zone. By 1989, attractions at the culturally rich Albert Dock complex alone
747 drew 3.5 million visitors, showcasing a blend of heritage preservation, waterfront
748 attractiveness, and vibrant aquatic ecosystems (West, 2022).
749

750 This successful restoration contributed significantly to Liverpool being designated a
751 UNESCO World Heritage Site (Liverpool Maritime Mercantile City) in 2004 and hosting

752 the European Capital of Culture in 2008. These accolades boosted tourism and spurred
753 investment in the city. However, the World Heritage status was rescinded in 2021 due
754 to modernist development encroaching on the historic landscape, including proposed
755 plans for a football stadium on a disused dock site.
756
757 Research increasingly demonstrates that urban regeneration projects improve mental
758 and physical well-being by providing spaces for social integration and mental
759 restoration, particularly benefiting communities of lower socioeconomic status (Baba
760 et al., 2017; EEA, 2020; Teixeria and Fernandes, 2020; Ward Thompson et al., 2016).
761 In our urbanizing world, these novel ecosystems should be integrated into
762 management strategies to optimize their multifunctional benefits, enhancing
763 connections between people and nature.
764
765 **Acknowledgements**
766 Support for this work in the 1970s and 1980s came from the Mersey Dock and
767 Harbour Company, the Merseyside Development Corporation, and the UK Nature
768 Conservancy Council. The 2012 research received funding from the Natural
769 Environment Research Council National Facility for Scientific Diving (NFSD, awarded
770 to LBF and SJH) and the Esmée Fairbairn Foundation (Urbane Project). Data analysis
771 was supported by student bursaries from the Marine Biological Association of the UK
772 (SJH). We thank Hugh Brown, Simon Thurston, and Elaine Azzopardi of the NFSD for
773 their assistance with dive surveys, and Andrew Mogg from NFSD for collating and
774 analyzing the photo-quadrats. We also thank Andy Goudie (Canal and Rivers Trust)

775 and Eilir Morgan, John Bishop, and Moira MacLean for their fieldwork support. SJH
776 acknowledges Tony Bradshaw for his guidance in restoration ecology.

777

778 **CRediT author statement**

779 Louise Firth: Data curation, Funding acquisition, Supervision, Writing-original draft.
780 Anastasia Forbes, Wahaj Mahmood Brown, Lewis Struthers, Ellie Hawcutt, Katrin
781 Bohn, Martin Sayer, James Quinn, Janette Allen, Simone Dürr, Maria Teresa Guerra,
782 Alexandra Leeper, Geraldine Reid, Stephen Wilkinson, Stephen J. Hawkins:
783 Investigation, Writing-review & editing. Antony Knights, Kathryn A. O'Shaughnessy:
784 Analysis, Writing original draft.

785

786 **Literature Cited**

787 Airoldi, L., Beck, M. W., Firth, L. B., Bugnot, A., Steinberg, P. A., Dafforn, K. A. 2021.
788 Emerging solutions to return nature to the urban ocean. Annual Review of Marine
789 Science, 13, 445-477. https://doi.org/10.1146/annurev-marine-032020-020015

790

791 Allen, J.R. 1992. Hydrography, ecology and water quality management of the South
792 Docks, Liverpool. University of Liverpool.

793

794 Allen, J.R., Hawkins, S.J., Russell, G.R., White, K.N. 1992. Eutrophication and urban
795 renewal: problems and perspectives for the management of disused docks. Marine
796 Coastal Eutrophication, 48, 1283-1295. https://doi.org/10.1016/B978-0-444-89990-
797 3.50108-5

798

799 Allen, J. R., Hawkins, S.J. 1993. Can biological filtration be used to improve water
800 quality? In: K. N. White, E. G. Belling, A. J. Saul, M. Symer & K. Hendry (Eds.), Urban
801 waterside regeneration, problems and prospects. Ellis Horwood. UK, 377–385.
802
803 Allen, J.R., Wilkinson, S.B., Hawkins, S.J. 1995. Redeveloped docks as artificial
804 lagoons: The development of brackish-water communities and potential for
805 conservation of lagoonal species. Aquatic Conservation: Marine and Freshwater
806 Ecosystems, 5, 299–309. https://doi.org/10.1002/aqc.3270050405
807
808 Baba, C., Kearns, A., McIntosh, E., Tannahill, C., Lewsey, J. 2017. Is empowerment a
809 route to improving mental health and wellbeing in an urban regeneration (UR)
810 context?. Urban studies, 54, 1619-1637. https://doi.org/10.1177/004209801663243
811
812 Bayraktarov, E., Saunders, M.I., Abdullah, S., Mills, M., Beher, J., Possingham, H.P.,
813 Mumby, P.J., Lovelock, C.E. 2016. The cost and feasibility of marine coastal
814 restoration. Ecological Applications, 26, 1055-1074. https://doi.org/10.1890/15-1077
815
816 Bishop, M.J., Vozzo, M.L., Mayer-Pinto, M., Dafforn, K.A. 2022. Complexity–
817 biodiversity relationships on marine urban structures: reintroducing habitat
818 heterogeneity through eco-engineering. Philosophical Transactions of the Royal
819 Society B, 377, 20210393. https://doi.org/10.1098/rstb.2021.0393
820

821 Bracewell, S.A., Clark, G.F., Johnston, E.L. 2018. Habitat complexity effects on
822 diversity and abundance differ with latitude: an experimental study over 20 degrees.
823 Ecology, 99(9), 1964–1974. https://www.jstor.org/stable/26626198
824
825 Bugnot, A.B., Mayer-Pinto, M., Airoldi, L., Heery, E.C., Johnston, E.L., Critchley, L.P.,
826 Strain, E.M.A., Morris, R.L., Loke, L.H.L., Bishop, M.J., Sheehan, E.V. 2021. Current
827 and projected global extent of marine built structures. Nature Sustainability, 4, 33-
828 41. https://doi.org/10.1038/s41893-020-00595-1
829
830 Bulleri, F., Batten, S., Connell, S.D., Benedetti-Cecchi, L., Gibbons, M., Nugues, M.M.,
831 Gribben, P. 2020. Human pressures and the emergence of novel marine ecosystems.
832 Oceanography and Marine Biology: an Annual Review, 58, 456-535.
833
834 Canal and River Trust. 2021. Liverpool's docks scoop England's 1st Blue Flag Marina
835 Award. https://canalrivertrust.org.uk/news-and-views/news/liverpools-docks-
836 scoop-englands-1st-blue-flag-marina-award Viewed 16/03/2023
837
838 Canal and River Trust. 2022. Liverpool's historic docks awarded Blue Flag Marina
839 Award. https://canalrivertrust.org.uk/news-and-views/news/liverpools-historic-
840 docks-awarded-blue-flag-marina-award Viewed 16/03/2023
841
842 Chee, S.Y., Othman, A.G., Sim, Y.K., Adam, A.N.M., Firth, L.B. 2017. Land reclamation
843 and artificial islands: Walking the tightrope between development and conservation.

844 Global Ecology and Conservation, 12, 80-95.

845 https://doi.org/10.1016/j.gecco.2017.08.005

846

847 Chee, S.Y., Yee, J.C., Cheah, C.B., Evans, A.J., Firth, L.B., Hawkins, S.J., Strain, E.M.A.

848 2021. Habitat complexity affects the structure but not the diversity of sessile

849 communities on tropical coastal infrastructure. Frontiers in Ecology and Evolution, 9,

850 673227. https://doi.org/10.3389/fevo.2021.673227

851

852 Clarke, K.R., Warwick, R.M. 1994. PRIMER: Plymouth Routines in Multivariate

853 Ecological Research, a Suite of Computer Programmes (Plymouth: Plymouth Marine

854 Laboratory).

855

856 Cloern, J.E. 1999. The relative importance of light and nutrient limitation of

857 phytoplankton growth: a simple index of coastal ecosystem sensitivity to nutrient

858 enrichment. Aquatic Ecology, 33, 3-15. https://doi.org/10.1023/A:1009952125558

859

860 Dafforn, K.A., Glasby, T.M., Airoldi, L., Rivero, N.K., Mayer-Pinto, M., Johnston, E.L.,

861 2015. Marine urbanization: an ecological framework for designing multifunctional

862 artificial structures. Frontiers in Ecology and the Environment, 13(2), 82-90.

863 https://doi.org/10.1890/140050

864

European Environmental Agency, EEA, 2020. Healthy environment, healthy lives: how the environment influences health and well-being in Europe. Luxembourg: European Environmental Agency.

Evans, A.J., Moore, P.J., Firth, L.B., Smith, R.K., Sutherland, W.J. 2021 Enhancing the Biodiversity of Marine Artificial Structures: Global Evidence for the Effects of Interventions. Conservation Evidence Series Synopses. University of Cambridge, Cambridge, UK.

Fariñas-Franco, J.M., Cook, R.L., Gell, F.R., Harries, D.B., Hirst, N., et al. 2023. Are we there yet? Management baselines and biodiversity indicators for the protection and restoration of subtidal bivalve shellfish habitats. Science of the Total Environment, 863, 161001. https://doi.org/10.1016/j.scitotenv.2022.161001

Fielding, N. 1997. Fish and Benthos Communities in Regenerated Dock Systems on Merseyside, PhD thesis, University of Liverpool, Liverpool.

Firth, L.B., Thompson, R.C., White, F.J., Schofield, M., Skov, M.W., et al. 2013. The importance of water-retaining features for biodiversity on artificial intertidal coastal defence structures. Diversity and Distributions, *19*(10), 1275-1283. https://doi.org/10.1111/ddi.12079

887 Firth, L.B., Duff, L., Gribben, P.E., Knights, A.M. 2021. Do positive interactions
888 between marine invaders increase likelihood of invasion into natural and artificial
889 habitats?. Oikos, 130(3), 453-463. https://doi.org/10.1111/oik.07862
890
891 Firth, L.B., Bone, J., Bartholomew, A., Bishop, M., Bugnot, A., et al. 2024. Coastal
892 greening of grey infrastructure: An update on the state-of-the-art. Proceedings of
893 the Institution of Civil Engineers - Maritime Engineering, 177, 35-67.
894 *https://doi.org/10.1680/jmaen.2023.003*
895
896 Hawkins, S.J., Allen, J.R., Russell, G., White, K.N., Conlan, K., Hendry, K. Jones, H.D.
897 1992a. Restoring and managing disused docks in inner city areas. In: Thayer, G. (Ed.)
898 Restoring the Nation's Marine Environment. 473-542.
899
900 Hawkins, S.J., Cunningham, P.N., Dolan, B., Evans, L.C., Holmes, G.D., O'Hara, K.,
901 Russell, G., Walmsley, A., White, K.N. 1992b. Culture of mussels in Sandon dock, a
902 disused dock basin in Liverpool. Journal of Medical and Applied Malacology, 4, 165-
903 178.
904
905 Hawkins, S.J., Allen, J.R., Russell, G., Eaton, J.W., Wallace, I., Jones, K.N., White, K.N.,
906 Hendry, K. 1993. Former commercial docks as a resource in urban conservation and
907 education, in White, K.N., Bellinger, E.G., Saul, A.J., Symer, M. and Hendry, K. (Eds),
908 Urban Waterside Regeneration Problems and Prospects, Ellis Horwood, UK, 386–
909 399.

Hawkins, S.J., Allen, J.R., Bray, S. 1999. Restoration of temperate marine and coastal ecosystems: nudging nature. Aquatic Conservation: Marine and Freshwater Ecosystems, 9, 23-46. https://doi.org/10.1002/(SICI)1099-0755(199901/02)9:1<23::AID-AQC324>3.0.CO;2-C

Hawkins, S.J., Vale, M., Firth, L.B., Burrows, M.T., Mieszkowska, N., Frost, M. 2013. Sustained observation of marine biodiversity and ecosystems. Oceanography, 1(1). https://doi.org/10.4172/2332-2632.1000e101

Hawkins, S.J., O'Shaughnessy, K.A., Adams, L.A., Langston, W.J., Bray, S., Allen, J.R., Wilkinson, S., Bohn, K., Mieszkowska, N., Firth, L.B. 2020. Recovery of an urbanised estuary: Clean-up, de-industrialisation and restoration of redundant dock-basins in the Mersey. Marine Pollution Bulletin, 156, 111150. https://doi.org/10.1016/j.marpolbul.2020.111150

Hendry, K., Conlan, K., White, K., Bewsher, A., Hawkins, S.J. 1988. Disused docks as a habitat for estuarine fish: a nationwide appraisal. Journal of Fish Biology, 33, 239-241. https://doi.org/10.1111/j.1095-8649.1988.tb05582.x

Hobbs, R.J., Higgs, E., Harris, J.A. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology & Evolution, 24(11), 599-605. https://doi.org/10.1016/j.tree.2009.05.012

Hughes, D.J., Cook, E.J., Sayer, M.D. 2005. Biofiltration and biofouling on artificial structures in Europe: the potential for mitigating organic impacts. Oceanography and Marine Biology: an Annual Review, 43, 133-182.

Jackson-Bué, T., Evans, A.J., Lawrence, P.J., Brooks, P.R., Ward, S.L., Jenkins, S.R., Moore, P.J., Crowe, T.P., Neill, S.P. Davies, A.J. 2023. Habitat structure shapes temperate reef assemblages across regional environmental gradients. Science of The Total Environment, 906, 167494. https://doi.org/10.1016/j.scitotenv.2023.167494

Janis, S., Birney, L., Newton, R. 2016. Billion oyster project: linking public school teaching and learning to ecological restoration of New York Harbor using innovative applications of environmental and digital technologies. International Journal of Digital Content Technology and its Applications, 10(1).

Thomas Kiran, M., Archana, T., Bhaskar, M.V. 2015. A new novel solution to grow diatom algae in large natural water bodies and its impact on CO_2 capture and nutrient removal. Journal of Algal Biomass Utilization, 6(2), 22-27.

Kautsky, N. 1982. Growth and size structure in a Baltic *Mytilus edulis* population. Marine Biology, 68, 117-133. https://doi.org/10.1007/BF00397599

955 Knights, A.M. 2012. Spatial variation in body size and reproductive condition of
956 subtidal mussels: considerations for sustainable management. Fisheries Research,
957 113(1), 45-54. https://doi.org/10.1016/j.fishres.2011.09.002
958
959 Layman, C.A., Jud, Z.R., Archer, S.K., Riera, D. 2014. Provision of ecosystem services
960 by human-made structures in a highly impacted estuary. Environmental Research
961 Letters, 9(4), 044009. https://doi.org/10.1088/1748-9326/9/4/044009
962
963 Lemasson, A.J., Somerfield, P.J., Schratzberger, M., Thompson, M.S., Firth, L.B.,
964 Couce, E., McNeill, C.L., Nunes, J., Pascoe, C., Watson, S.C., Knights, A.M. 2024. A
965 global meta-analysis of ecological effects from offshore marine artificial structures.
966 Nature Sustainability, 7, 485-495. https://doi.org/10.1038/s41893-024-01311-z
967
968 Markager, S., Sand-Jensen, K. 1992. Light requirements and depth zonation of
969 marine macroalgae. Marine Ecology Progress Series, 88, 83-83.
970
971 Mayer-Pinto, M., Caley, A., Knights, A.M., Airoldi, L., Bishop, M.J., Brooks, P.,
972 Coutinho, R., Crowe, T., Mancuso, P., Naval-Xavier, L.P., Firth, L.B. 2024. Complexity-
973 functioning relationships differ across different environmental conditions. Journal of
974 Environmental Management, 354, 120370.
975 https://doi.org/10.1016/j.jenvman.2024.120370
976

977 McFarland, K., Hare, M.P. 2018. Restoring oysters to urban estuaries: Redefining
978 habitat quality for eastern oyster performance near New York City. PloS One, 13(11),
979 e0207368. https://doi.org/10.1371/journal.pone.0207368
980
981 Mieszkowska, N., Sugden, H., Firth, L.B., Hawkins, S.J. 2014. The role of sustained
982 observations in tracking impacts of environmental change on marine biodiversity
983 and ecosystems. Philosophical Transactions of the Royal Society A: Mathematical,
984 Physical and Engineering Sciences, 372, 20130339.
985 https://doi.org/10.1098/rsta.2013.0339
986
987 Morris, R.L., Bilkovic, D.M., Boswell, M.K., Bushek, D., Cebrian, J., Goff, J., Kibler,
988 K.M., La Peyre, M.K., McClenachan, G., Moody, J., Sacks, P., 2019. The application of
989 oyster reefs in shoreline protection: Are we over-engineering for an ecosystem
990 engineer?. Journal of Applied Ecology, 56(7), 1703-1711.
991 https://doi.org/10.1111/1365-2664.13390
992
993 Morris, R.L., La Peyre, M.K., Webb, B.M., Marshall, D.A., Bilkovic, D.M., Cebrian, J.,
994 McClenachan, G., Kibler, K.M., Walters, L.J., Bushek, D., Sparks, E.L. 2021. Large-scale
995 variation in wave attenuation of oyster reef living shorelines and the influence of
996 inundation duration. Ecological Applications, 31(6), e02382.
997 https://doi.org/10.1002/eap.2382
998

999 O'Shaughnessy, K.A., Hawkins, S.J., Evans, A.J., Hanley, M.E., Lunt, P., Thompson,
1000 R.C., Francis, R.A., Hoggart, S.P., Moore, P.J., Iglesias, G., Simmonds, D., Ducker, J.,
1001 Firth, L.B. 2020. Design catalogue for eco-engineering of coastal artificial structures:
1002 a multifunctional approach for stakeholders and end-users. Urban Ecosystems,
1003 23(2), 431-443. https://doi.org/10.1007/s11252-019-00924-z
1004
1005 O'Shaughnessy, K.A., Perkol-Finkel, S., Strain, E., Bishop, M., Hawkins, S.J., Hanley,
1006 M.E., Lunt, P., Thompson, R.C., Yunnie, A.L.E., Amstutz, A., Milliet, L., Yong, C., Firth,
1007 L.B. 2021. Spatially variable effects of artificially-created physical complexity on
1008 subtidal benthos. Frontiers in Ecology and Evolution, 9, 690413.
1009 https://doi.org/10.3389/fevo.2021.690413
1010
1011 O'Shaughnessy, K.A., Knights, A.M., Hawkins, S.J., Hanley, M.E., Lunt, P., Thompson,
1012 R.C., Firth, L.B. 2023. Metrics matter: Multiple diversity metrics at different spatial
1013 scales are needed to understand species diversity in urban environments. Science of
1014 the Total Environment, 895, 164958.
1015 https://doi.org/10.1016/j.scitotenv.2023.164958
1016
1017 Rezek, R.J., Furman, B.T., Jung, R.P., Hall, M.O., Bell, S.S. 2019. Long-term
1018 performance of seagrass restoration projects in Florida, USA. Scientific Reports, 9(1),
1019 1-11. https://doi.org/10.1038/s41598-019-51856-9
1020

1021 Ritchie-Noakes, N. 1984. Liverpool's historic waterfront. The world's first mercantile
1022 dock system. Royal Commission on Historical Monuments, Supplementary Series, 7.
1023
1024 Rosenzweig, M.L. 2003. Win-win ecology: how the earth's species can survive in the
1025 midst of human enterprise. Oxford University Press.
1026
1027 Russell, G., Hawkins, S.J., Evans, L.C., Jones, H.D., Holmes, G.D. 1983. Restoration of a
1028 disused dock basin as a habitat for marine benthos and fish. Journal of Applied
1029 Ecology, 20, 43-58. https://doi.org/10.2307/2403375
1030
1031 Safak, I., Norby, P.L., Dix, N., Grizzle, R.E., Southwell, M., Veenstra, J.J., Acevedo, A.,
1032 Cooper-Kolb, T., Massey, L., Sheremet, A., Angelini, C. 2020. Coupling breakwalls
1033 with oyster restoration structures enhances living shoreline performance along
1034 energetic shorelines. Ecological Engineering, 158, 106071.
1035 https://doi.org/10.1016/j.ecoleng.2020.106071
1036
1037 Schneider, C.A., Rasband, W.S., Eliceiri, K.W. 2012. NIH Image to ImageJ: 25 years of
1038 image analysis. Nature Methods, 9, 671-675. https://doi.org/10.1038/nmeth.2089
1039
1040 Seed, R. 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky
1041 shores: II. Growth and mortality. Oecologia, 3, 317-350.
1042 https://doi.org/10.1007/BF00390381
1043

1044 Seitz, B., Buchholz, S., Kowarik, I., Herrmann, J., Neuerburg, L., Wendler, J., Winker,
1045 L., Egerer, M. 2022. Land sharing between cultivated and wild plants: urban gardens
1046 as hotspots for plant diversity in cities. Urban Ecosystems, 25(3), 927-939.
1047 https://doi.org/10.1007/s11252-021-01198-0
1048
1049 Sheath, R.G., Wehr, J.D. 2015. Introduction to the Freshwater Algae. In Freshwater
1050 Algae of North America (pp. 1–11). Academic Press.
1051
1052 Smaal, A.C., Verbagen, J.H.G., Coosen, J., Haas, H.A. 1986. Interaction between
1053 seston quantity and quality and benthic suspension feeders in the Oosterschelde,
1054 The Netherlands. Ophelia, 26(1), 385-399.
1055 https://doi.org/10.1080/00785326.1986.10422002
1056
1057 Soga, M., Gaston, K.J. 2018. Shifting baseline syndrome: causes, consequences, and
1058 implications. Frontiers in Ecology and the Environment, 16(4), 222-230.
1059 https://doi.org/10.1002/fee.1794
1060
1061 Sousa, W.P. 1979. Experimental investigations of disturbance and ecological
1062 succession in a rocky intertidal algal community. Ecological Monographs, 49(3), 227-
1063 254. https://doi.org/10.2307/1942484
1064

1065 Steffani, C.N., Branch, G.M. 2003. Growth rate, condition, and shell shape of *Mytilus*
1066 *galloprovincialis*: responses to wave exposure. Marine Ecology Progress Series, 246,
1067 197-209. https://doi.org/10.3354/meps246197
1068
1069 Strain, E.M., Olabarria, C., Mayer-Pinto, M., Cumbo, V., Morris, R.L., Bugnot, A.B.,
1070 Dafforn, K.A., Heery, E., Firth, L.B., Brooks, P.R., Bishop, M.J. 2018. Eco-engineering
1071 urban infrastructure for marine and coastal biodiversity: which interventions have
1072 the greatest ecological benefit?. Journal of Applied Ecology, 55(1), 426-441.
1073 https://doi.org/10.1111/1365-2664.12961
1074
1075 Strain, E.M., Steinberg, P.D., Vozzo, M., Johnston, E.L., Abbiati, M., Aguilera, M.A.,
1076 Airoldi, L., Aguirre, J.D., Ashton, G., Bernardi, M., Brooks, P. 2021. A global analysis of
1077 complexity–biodiversity relationships on marine artificial structures. Global Ecology
1078 and Biogeography, 30(1), 140-153. https://doi.org/10.1111/geb.13202
1079
1080 Struthers, L. 2022. Persistence and Stability of a Novel Ecosystem in the South Dock
1081 Complex, Liverpool. MSc thesis, University of Liverpool.
1082
1083 Teixeira, C.P., Fernandes, C.O. 2020. Novel ecosystems: a review of the concept in
1084 non-urban and urban contexts. Landscape Ecology, 35(1), 23-39.
1085 https://doi.org/10.1007/s10980-019-00934-4
1086

1087 Tomatsuri, M., Kon, K. 2017. Effects of dead oyster shells as a habitat for the benthic
1088 faunal community along rocky shore regions. Hydrobiologia, 790, 225-232.
1089 https://doi.org/10.1007/s10750-016-3033-y
1090
1091 Wanstall, V.C. 1997. Monitoring, manipulation and management of the Liverpool
1092 Docks. Master in Philosophy, University of Liverpool.
1093
1094 Ward Thompson, C., Aspinall, P., Roe, J., Robertson, L., Miller, D. 2016. Mitigating
1095 stress and supporting health in deprived urban communities: the importance of
1096 green space and the social environment. International Journal of Environmental
1097 Research and Public Health, 13(4), 440. https://doi.org/10.3390/ijerph13040440
1098
1099 West, T. 2022. Liverpool's European Capital of Culture legacy narrative: a selective
1100 heritage?. European Planning Studies, 30(3), 534-553.
1101 https://doi.org/10.1080/09654313.2021.1959725
1102
1103 Wilkinson, S.B. 1995. The ecology of disused dock basins. PhD thesis, University of
1104 Liverpool, Liverpool.
1105
1106 Wilkinson, S.B., Zheng, W., Allen, J.R., Fielding, N.J., Wanstall, V.C., Russell, G.,
1107 Hawkins, S.J. 1996. Water quality improvements in Liverpool docks: the role of filter
1108 feeders in algal and nutrient dynamics. Marine Ecology, 17(1-3), 197-211.
1109 https://doi.org/10.1111/j.1439-0485.1996.tb00501.x

Williams, A. 2005. The Theory of Alternative Stable States in Shallow Lake Ecosystems. In Water Encyclopedia, Wiley Publishers. https://doi.org/10.1002/047147844X.sw24

Yachi, S., Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proceedings of the National Academy of Sciences, 96(4), 1463–1468. https://doi.org/10.1073/pnas.96.4.1463

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	**

1124 Table 2. Summary of the minimum, maximum and mean values for each physico-
1125 chemical parameter measured at the surface or 1m above the bottom in Albert and
1126 Queens Docks across the summer months (June-August) during the whole survey
1127 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

1128

1129

1130