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Changing bryozoan fauna in Otago Harbour reflects growing urbanisation and globalisation

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ABSTRACT

A comparison between historic reports dating from 1884 (78 records of 35 species) to the bryozoan fauna present today (98 colonies of 14 species) reveals considerable faunal change in Otago Harbour / Te Wai Ōtākou (45° 50′S 170° 38′E) in Dunedin, east coast of South Island, Aotearoa New Zealand. This highly-modified urban port was once a rock-edged tidal inlet surrounded by bush and grassy hills, but changes to its flora and fauna are not limited to land and the intertidal. Our modern bryozoan surveys record predominantly 'weedy' invasive species which colonise anthropogenic surfaces, while previously-recorded larger, slower-growing native species are now missing. This study emphasises the importance of historical data and regular monitoring in determining baselines for conservation and restoration.

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Introduction

In the nineteenth century it was common for regional journals to publish detailed surveys of fauna present in particular locations (e.g. Hutton 1878; Waters 1887), especially in the far-flung outposts of the British Empire. Once 'exotic' faunas were documented and described, preliminary census-type research gave way to more question-focussed and system-based science. But there is a place for species lists in modern science, particularly in a place where there is data available throughout a period of human development.

Aotearoa New Zealand was the last significant land mass on Earth to be settled by humans, and thus lends itself to investigation of human impacts on native ecosystems. Inhabited by Māori since about 1200–1300 AD, it was not 'discovered' by Europeans until the mid-1600s. Many studies have examined the land-based changes in fauna and flora which have occurred since human occupation (e.g. Bathgate 1922; Star 1998), but there are few analogous historical approaches to the marine environment (but see MacDiarmid et al. 2016).

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Here we compare historical and modern surveys of marine bryozoans in Otago Harbour, Dunedin, New Zealand, supplementing published information from 1897 to 2020 with new surveys carried out in 2021–2023. In addition to providing a comprehensive list of the past and present bryozoan fauna in Otago Harbour, we analyse trends in bryozoan species diversity.

Bryozoans

Bryozoans are a phylum of largely colonial sessile attached intertidal and subtidal benthic marine invertebrates, though there are freshwater species (e.g. Ko 2019), and even a few unattached non-sessile Bryozoa (Hageman et al. 1997; Hageman et al. 1998; Hermansen et al. 2001). Bryozoan colonies are made up of individual animals called zooids (Lidgard and Jackson 1989; Hageman et al. 1998). Autozooids are the most abundant of these, and are responsible for feeding (Okamura et al. 2011); in contrast heterozooids are non-feeding zooids that may play a role in reproduction, defence, or motility (Serova et al. 2017; Schack et al. 2019; Schack et al. 2020).

Bryozoans are lophotrochozoans; they feed by generating a current that draws suspended particles into contact with tentacles on a muscular ring, called a lophophore (Sun et al. 2009; Okamura et al. 2011). Most marine bryozoans are calcified, growing a biomineralised skeleton for protection and support (Hageman et al. 1998; Steger and Smith 2005; Smith et al. 2006; Loxton et al. 2018). They generally grow on hard surfaces, including rocks, hard-shelled animals, boats, wood, and anthropogenic objects, growing on undersides and in darkness, and are very seldom found on mud and sandy-bottom environments (Mackie et al. 2014; Li et al. 2016). Bryozoans can occur as epibionts on many organisms including: macroalgae, sponges, molluscs, and even crayfish (Piazzi et al. 2015; Key et al. 2023). Bryozoan predators include nudibranchs, pycnogonids, and fish (Seed 1976; Linneman et al. 2014).

Bryozoans are essential components of biodiversity, particularly in the temperate Southern Hemisphere (Smith 2014). They provide both habitat stabilisation by encrusting over loose substrate (Hageman et al. 1998), and habitat space for other invertebrates and small fish in the form of bryozoan 'reefs' or thickets (Wood et al. 2013). In addition, bryozoan skeletons contribute to the formation of sediment and sequestering of carbon (Smith 2014).

Otago Harbour

Otago Harbour / Te Wai Ōtākou (45° 50'S 170° 38'E) is a sheltered tidal inlet of volcanic origin which houses the port for Ōtepoti Dunedin, located on the east coast of the South Island, Aotearoa New Zealand (Figure 1). As the closest naturally sheltered anchorage is 360 km to the north, it has significant cultural and historical importance (Carter 2012). The Harbour is roughly 23 km long, with an average width of 2 km and a total area of 46 km^2. It lies on a NE-SW axis, and the harbour mouth, with Taiaroa Head to the south and Aramoana to the north, is only 0.4 km wide (Grove and Probert 1999). The harbour is relatively shallow and well-mixed, with an average depth of 4.5 m, though a shipping channel with a minimum depth of 12 m dominates tidal flow in the area (Croot and Hunter 2000; Smith et al. 2010); the tidal range is about 2.1 m. Though there are

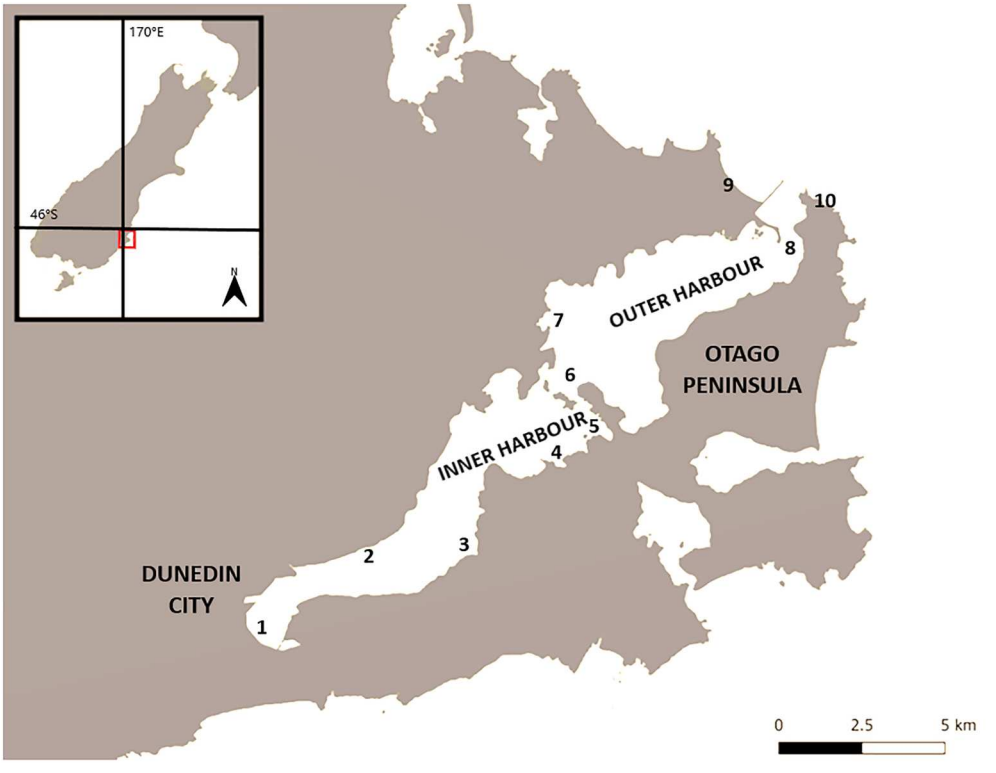

Figure 1. Map of Otago Harbour, showing Dunedin City and Otago Peninsula. Survey locations indicated with numbers: City Wharves (1). Ravensbourne (2), Macandrew Bay (3), Broad Bay (4), Quarantine Island (5), Portobello Marine Laboratory (6), Port Chalmers (7), Harrington Point (8).

intertidal sandflats near the entrance at Aramoana (Croot and Hunter 2000; Smith et al. 2010), and a few small artificial swimming beaches, most of the edge of the Harbour is modified by artificial rocky seawalls.

Otago Harbour has one main freshwater input; a small stream called the Water of Leith (Croot and Hunter 2000). The harbour is divided in two: the inner and outer harbour are separated by two peninsulas at Port Chalmers and Portobello. The inner harbour is shallow and muddy with a water residence time of 15–30 days (Croot and Hunter 2000; Smith et al. 2010), whereas the outer harbour is deeper with a water residence time of 12–24 h, with sea-grass ecosystems, and coarser sediments (Croot and Hunter 2000; Mills and Berkenbusch 2009; Smith et al. 2010). Salinities in the outer harbour range from 31 to 34, decreasing to as low as 29 and becoming more variable towards the inner harbour, (Grove and Probert 1999; Croot and Hunter 2000).

The Ōtākou area has been inhabited since approximately 1250 AD, settled by Māori tribes who took advantage of its plentiful marine life (Wells et al. 2019). Sealing, whaling, and anthropogenic modification has occurred during the last 800 or so years. European development of the city Ōtepoti Dunedin began in 1848, including modifications of the harbour by dredging, shoreline construction, pollution (including 43 shipwrecks) and land appropriation of almost 4 km^2 (Smith et al. 2010; Carter 2012). The population of Dunedin has grown substantially over this time (Thorns and Schrader 2024; Infometrics 2023).

A natural tidal inlet that has been heavily modified into a port and harbour by human occupation, especially over the last 150 years, Otago Harbour offers the opportunity to examine the impacts of coastal development on shallow-water invertebrates.

Definitions of terms used within the text

Cosmopolitan: a species with a substantial range, typically species referred to a cosmopolitan in this study have a documented range encompassing New Zealand and Australia.

Encrusting: to grow on the surface of something, encrusting bryozoans in this study grow on a variety of substrates.

Exotic: a species foreign to a region, in this case Otago Harbour, used interchangeably with invasive in this text, though there are typically differences between the two terms. The two major exotic species in this text are *Bugulina flabellata* (origin the Gulf of Mexico), and *Watersipora subatra* (origin unknown but thought to be somewhere in Asia).

Fouling: a species that grows on anthropogenic structures such as boats, buoys, and wharves, typically affecting the structural or functional integrity of the object.

Invasive: a species foreign to a region, in this case Otago Harbour, used interchangeably with exotic in this text, though there are some differences between the two terms.

Native: a species that occurs in a region naturally, in this case Otago Harbour. Not to be confused with endemic, which is not used in this text.

Weedy: in this text weedy refers to a bryozoan with a branching, plant-like growth form.

Methods

Historical data

Historical records of bryozoans occurring within Otago Harbour were found through an extensive literature review. We accepted observations that recorded bryozoan colonies to at least genus level, recording precise location and date information where available. Data was found from as far back as the late 1800s (Hamilton 1897). Later data from the 1950s (Hurley 1954; Batham 1956) and 1960s (Rainer 1981) were followed by a survey from the 1990s (Gordon and Mawatari 1992). A biosecurity survey in 2003 focusing on the invasive taxa of Dunedin's Port Chalmers was included (Morrisey et al. 2007), and several papers from this decade also mentioned Bryozoa in Otago Harbour (Hepburn et al. 2006; Smith et al. 2010) A later survey of *Bugulina flabellata* in particular was conducted in 2017 (Davis 2017).

The collections of various institutions were consulted as well. Only one species was found in the NIWA collection, and no species were found in the collections of either Te Papa or Auckland Museum. Otago and Canterbury Museums, however, yielded a few specimens arguably found in Otago Harbour, though their labelling and identification was less than ideal.

Modern data

Monthly surveys were carried out in Otago Harbour beginning in early 2021 (Table 1). Particular attention was paid to the floating pontoon at Portobello Marine Laboratory

Table 1. Modern (2021–2023) bryozoan survey sampling programme, Otago Harbour, New Zealand.

Sampling Date		City Wharves (1)	Ravensbourne (2)	Macandrew Bay (3)	Inner Harbour Shipping Lane	Broad Bay (4)	Quarantine Island (5)	Portobello Marine Lab (6)	Port Chalmers (7)	Outer Harbour Shipping Lane	Harrington Point (8)
2021	February							X			
	March							X			
	April							X			
	May							X			
	June							X			
	July							X			
	August							X	X		
	September							X			
	October							X			
	November							X			X
	December							X			
2022	January	X						X			
	February							X			
	March							X			
	April							X			
	May							X			
	June							X			
	July							X			
	August							X			
	September							X			
	October				X		X	X	X	X	
2023	November	X	X	X	X	X		X			

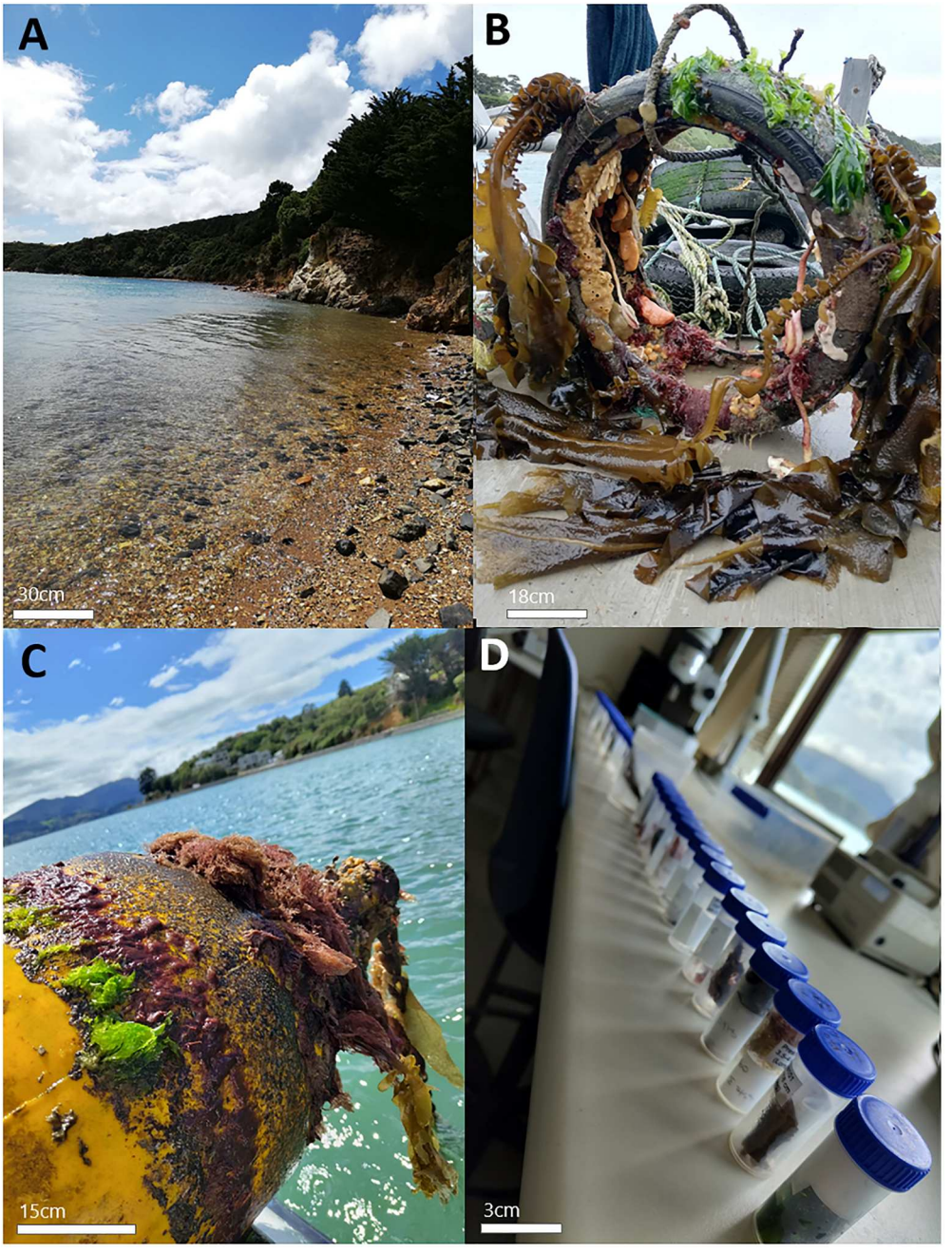

Figure 2. Photographs of bryozoan sampling locations: **A** Portobello Marine Laboratory beach, **B** tyres at Portobello Marine Laboratory, **C** a buoy being sampled at Anderson's Bay, **D** several samples lined up for processing and identification.

(−45.8278, 170.6405), as well as a set of four tires that have been hanging off the wharf in the water for several years, known to host bryozoan communities in the past. These areas were surveyed for bryozoans at least monthly for 22 months from February 2021 to

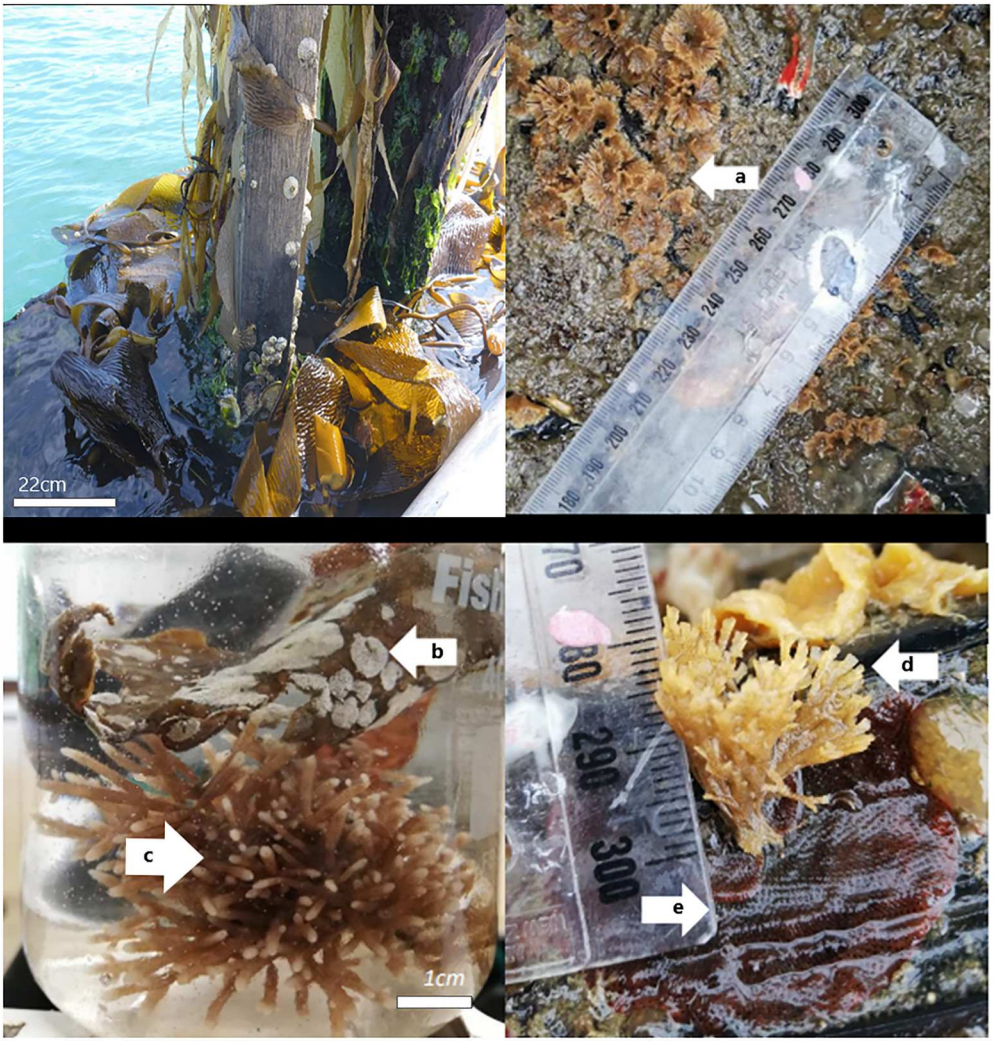

Figure 3. **A** wharf pile from the Harbour Shipping Lane A that was sampled during our surveys, **B** colonies of *Caberea zelandica*, **C** *Membranipora membranacea* living on a kelp blade, **D** *Elzerina binderi*, **E** *Bugulina flabellata* on a dark red encrusting colony of **F** *Watersipora subatra*.

October 2022 (Figure 2). Further *ad hoc* surveys occurred around the Harbour at Quarantine Island in March 2021 and Harrington Point beach in November 2021. The harbour piles along the main shipping lane in Otago Harbour were surveyed in October 2022, and Port Chalmers in late 2021 and again in late 2022. Sites along the shoreline of the inner harbour was surveyed in early 2022.

Finally, in November 2023 we conducted a detailed survey of the Portobello and inner harbour area. We sampled pylons along the shipping lane, wharf piles, and buoys.

Once a bryozoan colony was located, it was photographed *in-situ* and substrate type and location were recorded. A small subsample was then collected from each colony for photomicrography (Figure 3). Samples were bleached in a 10% bleach solution, dried and

then photographed again under a microscope. The colonies were identified using the works of Dennis Gordon (Gordon 1984; 1986), with names updated according to the World Register of Marine Species (WoRMS 2023). For larger specimens, material was split, and half was bleached and dried, and half preserved in 90% ethanol. A series of labelled slides of dried bryozoan material was made for easily comparing newly collected material with older material. All this material was labelled with species, date, location, and preservative information and stored at Portobello Marine Laboratory, Portobello, sorted by species, date, and location.

Results

Historical data

Bryozoans have been recorded living within Otago Harbour since 1897. Eleven publications date from Hamilton (1897) to Davis (2017). Our survey of historical collections yielded a further six records, housed at NIWA, Otago Museum, and Canterbury Museum. In total we have found 78 records of 35 species (a relatively rich fauna compared to other New Zealand ports (Gordon and Mawatari 1992)) from Otago Harbour since 1897 but species composition changed significantly over time (Table 2; Supplementary Data File).

Modern data

Ten sites in the Harbour were surveyed between February 2021 and November 2023. Ninety-eight bryozoan colonies from 14 species were collected, identified, and preserved (Table 3; Supplementary Data File). *Watersipora subatra* was most widespread, found throughout Otago Harbour (Figure 4). *Membranipora membranacea* was also distributed throughout most of Otago Harbour, though was less common. *Elzerina binderi* was found only in the outer harbour. A further 11 species were found much more patchily (Table 3).

We also took note of substrate preferences (Table 4). *Watersipora subatra* was, as expected in an invasive bryozoan, cosmopolitan; it was seen on tires, oyster and clam shells, and rock. *Elzerina binderi*, on the other hand, exclusively grew on the stalks of the ascidian *Pyura pachydermatina*. *Membranipora membranacea, Electra scutifera* and *Celleporina proximalis* were observed only encrusting on macroalgae. *Parasmittina delicatula* was observed encrusting only on tires. *Bugulina flabellata*, *Caberea zelandica*, *Smittoidea maunganuiensis* and *Beania* sp. were observed growing on both tires and shells. *Telopora lobata* was found on a fragment of *Hippomenella vellicata* washed up in the intertidal.

Populations of *Watersipora subatra* and *Caberea zelandica* were abundant, found in groups of up to 10+ colonies. *Beania* sp., *Elzerina binderi, Parasmittina delicatula, Smittoidea maunganuiensis, Membranipora membranacea* and *Bugulina flabellata* populations were less so, but still often seen in groups of up to five colonies. *Celleporina proximalis* and *Electra scuticifera* were each observed only as single colonies, and *Hippomenella vellicata* was only a fragment of a colony, with a single colony of *Telopora lobata* encrusted on it.

Most species were observed either as being solitary, or occurring within the presence of up to 6+ other bryozoan taxa. *Membranipora membranacea, Electra scuticifera* and *Celleporina proximalis* were observed only as solitary colonies (Table 4).

Table 2. Bryozoan species recorded 1884–2017 in Otago Harbour, New Zealand.

Species	Location	Date	Reference
Amphiblestrum blandum (Gordon 1986) N	Portobello	1986	NIWA Collection (#78150802)
Amathia biseriata (Krauss 1837) C	Otago Harbour	1897	Hamilton (1897)
Arachnopusia unicornis (Hutton 1873) C	Otago Harbour	1897	Hamilton (1897)
	Otago Harbour	1992	Gordon and Mawatari (1992)
Bugulina flabellata (Thompson in Gray 1848) E	Otago Harbour	1992	Gordon and Mawatari (1992)
	Portobello	2017	Davis (2017)
	Quarantine Island	2017	Davis (2017)
	Portobello	2017	Davis (2017)
	Broad Bay	2017	Davis (2017)
	Port Chalmers	2017	Davis (2017)
	City Wharves	2017	Davis (2017)
Bugula neritina (Linnaeus 1758) E	Otago Harbour	1992	Gordon and Mawatari (1992)
Caberea zelandica (Gray 1843) N	Otago Harbour	1965	Rainer (1981)
Calloporina angustipora (Hinks 1885) N	Otago Harbour	1992	Gordon and Mawatari (1992)
Celleporella (*Antarctothoa*) *bathamae* (Ryland & Gordon 1977) N	Otago Harbour	1992	Gordon and Mawatari (1992)
Celleporina granum (Hinks 1881) C	Otago Harbour	1965	Rainer (1981)
Celleporina proximalis (Uttley & Bullivant) N	Otago Harbour	1992	Gordon and Mawatari (1992)
Chaperiopsis cervicornis (Busk 1854) C	Otago Harbour	1992	Gordon and Mawatari (1992)
Chorizopora bronguiartii (Audouin 1826) C	Otago Harbour	1897	Hamilton (1897)
Cornuticella perforata (Busk 1852) C	Otago Harbour	1897	Hamilton (1897)
Costaticella bicuspis (Gray 1843) C	Otago Harbour	1897	Hamilton (1897)
Crassimarginatella solidula (Hinks 1860) C	Otago Harbour	1897	Hamilton (1897)
Cryptosula pallasiana (Moll 1803) E	Otago Harbour	1897	Hamilton (1897)
	Otago Harbour	1992	Gordon and Mawatari (1992)
Disporella spp. (Gray 1848) C	Portobello	2017	Davis (2017)
Elzerina binderi (Busk 1861) C	Portobello	2017	Davis (2017)
	Otago Harbour	1897	Hamilton (1897)
	Otago Harbour	1965	Rainer (1981)
	Otago Harbour	1897	Hamilton (1897)
Hippothoa (Celleporella) hyalina (Linnaeus 1767) C	Otago Harbour	2010	Smith et al. (2010)
Macropora similis (Gordon & Taylor 2008) N	Otago Harbour	1897	Hamilton (1897)
Membranipora (*Odontionella*) *cyclops* (Busk 1854) N	Otago Harbour	1897	Hamilton (1897)
Membranipora membranacea (Linnaeus 1767) C	Otago Harbour	1965	Rainer (1981)
	Otago Harbour	2010	Smith et al. (2010)
Orthoscuticella ventricosa (Busk 1852) C	Otago Harbour	1897	Hamilton (1897)
Paracribricellina cribraria (Busk 1852) C	Otago Harbour	1897	Hamilton (1897)
Parasmittina trispinosa (Johnston 1838) C	Otago Harbour	1897	Hamilton (1897)
Schizosmittina cinctipora (Hinks 1883) N	Otago Harbour	1992	Gordon and Mawatari (1992)
Watersipora subtorquata (d'Orbigny 1852) E	Carey's Bay	1992	Gordon and Mawatari (1992)
	Victoria Wharf	1992	Gordon and Mawatari (1992)

Note: Current species status from the World Register of Marine Species (N – native, C – cosmopolitan, E – exotic).

Statistical analyses

When formally analysing the data gathered on Otago Harbour's bryozoan fauna through time, the following trends were observed:

Table 3. Bryozoan species found in modern (2021–2023) surveys of Otago Harbour, New Zealand.

Bryozoan Species	City Wharves (1)	Ravensbourne (2)	Macandrew Bay (3)	Inner Harbour Shipping Lane	Broad Bay (4)	Quarantine Island (5)	Portobello Marine Lab (6)	Port Chalmers (7)	Outer Harbour Shipping Lane	Harrington Point (8)
Beania sp. C				X	X		X			
Bugulina flabellata E	X			X			X			
Caberea zelandica N							X			
Celleporina proximalis N				X			X			
Electra scuticifera N								X		
Elzerina binderi C							X	X	X	X
Hippomenella vellicata N							X			
Membranipora membranacea C		X		X			X	X	X	X
Parasmittina delicatula C							X			
Smittoidea maunganuiensis C							X			
Telopora lobata N							X			
Watersipora subatra E	X	X	X	X	X		X	X	X	
Unidentified ascidian/ bryozoan				X						
Unidentified transparent bryozoan				X						

Note: Current species status is also given using information from the World Register of Marine Species (N – native, C – cosmopolitan, E – exotic).

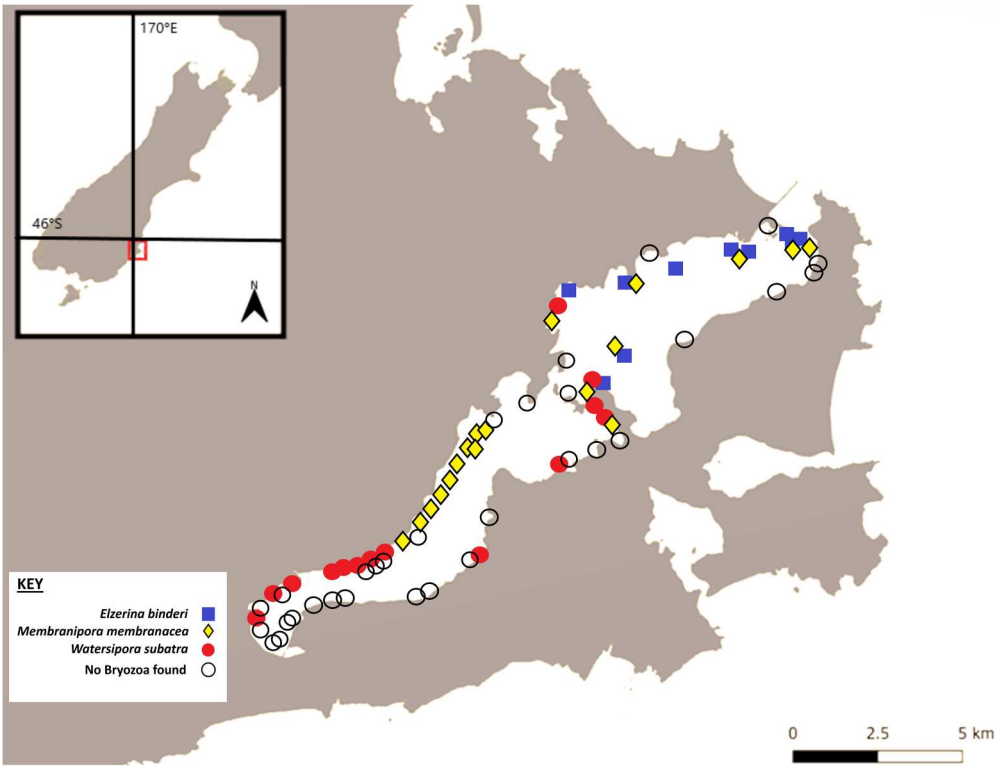

Figure 4. Modern distribution of the three most commonly observed bryozoan taxa within Otago Harbour: *Elzerina binderi* (blue squares), *Watersipora subatra* (red circles), and *Membranipora membranacea* (yellow diamonds). Locations surveyed but where these species were not found are indicated by open circles. Sampled 2021–2023.

The Shannon Diversity of an ecosystem can be calculated by recording not only species richness, but also the population sizes of those species (Daly et al. 2018). Because many of the previous surveys lack information on population sizes, the Shannon Diversity could only be accurately calculated for our modern (2021–2023) surveys. The result for Otago Harbour 2021–2023 was a Shannon-Diversity index of 2.06, with an evenness of 0.781. An index of zero would indicate there is no diversity present, and a typical index falls between 1.5 and 3.5. Evenness is also a measure of diversity, the closer it is to 1, the higher the ecosystem's diversity (Daly et al. 2018).

Species richness of the 1897 survey was 13 species, the 1992 survey was 10 species, and the 2021–2023 surveys totalled 14 species. Excluding exotic and cosmopolitan taxa, the 1897 species richness was 2, species richness for 1992 was 4, and species richness for 2021–2023 was 5. While this results is seemingly opposite to our previous observations, refinements in taxonomic understanding can result in species richness increasing over time.

The area of Otago Harbour is approximately 46 km^2, using this we can calculate a very basic value for species richness by area by dividing the number of species by this area.

1897: 13/46 = 0.283 species per kilometre.

1992: 10/46 = 0.217 species per kilometre.

2021–2023: 14/46 = 0.304 species per kilometre.

Table 4. Substrate, timing and number of colonies for bryozoan species found in 2021–2023 survey of Otago Harbour, New Zealand.

	Substrate					When found					Number of colonies				
Bryozoan Species	Tire	Shell	Macroalga	Rock	Ascidian	Early 2021	Late 2021	Early 2022	Late 2022	Late 2023	Single colony	2–5 colonies	5–10 colonies	10+ colonies	Fragment
Beania sp. C	X	X						X		X	X	X			
Bugulina flabellata E	X	X						X	X	X		X	X		
Caberea zelandica N	X	X				X	X	X	X		X	X	X	X	
Celleporina proximalis N			X			X				X	X				
Electra scuticifera N			X				X				X				
Elzerina binderi C					X		X		X	X	X				
Hippomenella vellicata N								X							X
Membranipora membranacea C			X			X	X	X	X	X		X	X	X	
Parasmittina delicatula C	X							X			X	X			
Smittoidea maunganuiensis C	X	X				X	X	X	X		X	X			
Telopora lobata N								X			X				
Watersipora subatra E	X	X		X		X	X	X	X	X	X	X	X	X	
Unidentified ascidian bryozoan					X					X		X			
Unidentified transparent bryozoan		X								X	X				

Note: Current species status ifrom the World Register of Marine Species (N – native, C – cosmopolitan, E – exotic).

Discussion

Otago Harbour – a changing environment

The history of Otago Harbour begins with the formation of a large shield volcano in the mid-Miocene (13–17 Mya), and its subsequent erosion into ridges separated by valleys. Two of these drowned valleys eventually merged to form a narrow waterway separating Otago Peninsula from the mainland. Accumulation of sediment at the southern end (now St Kilda and St Clair) formed a tombolo that closed off what we now call Otago Harbour between about 9000 and 6500 years PB (Carter 2011); sand also accumulated in a series of banks at the other end (off Taiaroa Heads). The inlet was naturally shallow with shifting sand banks and channels. Lowland areas now occupied by Dunedin City were marshy and regularly flooded. Intertidal and subtidal invertebrates, including bryozoans, would have lived on rocky outcrops and among kelp forests, possibly on seagrass beds.

It is believed that the first human explorers arrived to this area fairly early in the Māori settlement of Aotearoa, about 1300. Semi-permanent villages were established along most coastlines (Table 5). In Otago, a cool temperate climate with moderate rainfall supported forests and grasslands. Otago Harbour was a source of fish, seals, and shellfish (Wells et al. 2019), and so attracted seasonal and later permanent settlements.

There is considerable debate about the exact history of the various iwi (tribes) who settled here, fought with each other, and sometimes, settled down into a prosperous network of permanent or semi-permanent villages along the coastline, based on the abundant kaimoana (seafood) available. Middens reveal the products of fishing, eeling, whaling, sealing, birding, shellfish gathering, and use of a wide variety of plants. Trading was by sea, up and down the coast. While inland forests were burnt during this time, there is little evidence of catchment change around Otago Harbour (Wells et al. 2019).

European sealers arrived in the 1800s–1830s; records suggest they found the inlet to be a useful shelter but hazardous for navigation. Conflict between them and the locals erupted into the 'Sealers' War', about 1810–1823 (Table 5). In 1831, the Weller brothers established a whaling station, which grew into a thriving but fairly lawless shantytown community during that decade. In 1835 a measles and influenza outbreak killed many local people, predominantly Māori, altering the racial balance of the community.

It was the arrival of Scottish settlers in 1848 that began systematic European development of Dunedin ('the Edinburgh of the South'), and the consequent colonisation of Otago Harbour, obtained essentially by stealth from Kai Tāhu. The Harbour was first managed by the Provincial Government, then by the Otago Harbour Board which was established in 1847. Throughout the 1840s and 1850s, settlers arrived by schooner and barque. Areas of wetland and marsh, now known as 'The Flat' in southern Dunedin were drained, filled, and built up. Podocarp forests and tussock grasslands were cleared by burning for pastureland.

Boat traffic in Otago Harbour increased greatly with the discovery of gold inland in Central Otago in 1861. Dunedin went from being a sleepy Scottish/Māori town to New Zealand's largest and richest city in the course of a few months. Alluvial sluicings from the goldfields sent tonnes of sediment down rivers, particularly the Clutha River, just south of Otago Peninsula. Entrained in dominantly northwards currents, sediment

Table 5. Key events in the life of Otago Harbour.

1250–1300s	Arrival of Māori settlers, sealing and fishing, seasonal and short-term settlements at Otakou
Early 1800s	European sealers use harbour but don't settle
1810–1823	The Sealers' War, Europeans vs Māori
1826	First chart of Otago Harbour (James Herd), he called it Port Oxley
Nov 1831	Weller brothers establish whaling station at Te Umu Kuri, Wellers Rock
1830s–40s	Busiest whaling station in the south, large (and fairly lawless) European population
1844	Survey of harbour depths
1844	New Zealand Company purchased Otago Block from Ngai Tahu for £2,400
July 1847	Schooner *Perseverance* wrecked at Otakou
1848	Scottish settlers arrive on *John Wickliffe* and *Philip Laing*
1850	Survey of Otago Harbour, chart by Stokes
1853	Province of Otago established
1858	First shipment of wool to London from Dunedin
Mar 1859	Barque *Revival* wrecked at entrance to Otago Harbour
Aug 1859	Ship *Henbury* wrecked at Port Chalmers
1859	Provincial Council began dredging programme
1860	Seawall building begun near Portobello Andersons Bay causeway built by prisoners
1861	Gold discovered in Central Otago (gold rush 1861–1870)
1861	Province of Southland separated from Otago
Jan 1862	Barque *Genevieve* wrecked at entrance to Otago Harbour
Apr 1863	Schooner *Christina* wrecked at entrance to Otago Harbour
July 1863	Steamer *Pride of the Yarra* wrecked off Blanket Bay 'worst shipping tragedy ever to occur within the confines of Otago Harbour' (Collins 1995)
1865	Dunedin fails to secede from the North Island
1866	Chinese immigration to work in goldfields
1868	First dredger commissioned to dredge harbour, the *New Era*
1870–1872	Seawalls and embankment constructed, Blanket Bay to Dunedin for trains
June 1874	Otago Harbour Board established
1877	Second dredger built, the *Vulcan*
1881	Victoria channel dredged
Late 1800s	Wastewater reticulation – wastewater and stormwater both drain into Otago harbour
Feb 1882	First frozen meat cargo departs Port Chalmers aboard *Dunedin*
1882	Third dredger built in Scotland and delivered, named the *222*.
Jan 1884	Work starts on Aramoana mole
Nov 1887	Aramoana mole completed
1893	Women's suffrage petition – 1/3 of Dunedin's women signed, the highest proportion in the country
1889	Trade unions begin to be formed
Apr 1908	Oil launch *Matakana* wrecked at Pulling Point
Apr 1909	Ferry steamer *Matariki* wrecked at Portobello
1920s	Considerable reclamation at Logan Park (Pelichet Bay)
1925	New Zealand and South Seas International Exhibition (Logan Park)
1927–35	remedial work on Aramoana mole
1929	delivery of a new dredge, the *Otakou*, the largest bucket dredger in the Southern Hemisphere (Davis 2009)
1930s	Rock that impeded the channel blasted or excavated (at Goat Island)
1838–1943	Further seawalls built along Otago Harbour edges
1946	Otakou Fisheries company established
1950–1964	remedial work on Aramoana mole
1954–56	Roxburgh Dam on Clutha River (blocking sediment)
1961	first cruise ship arrives at Port Chalmers (the *Seven Seas)*
1966–67	Rock removed from Port Chalmers basin, Beach St wharf built
1960s to 1990s	Wastewater separated from stormwater system
June 1971	*Columbus NZ* departs PC, first cellular container ship
1970s	development of container terminal at PC, huge dredging programme
Mid-1970s	proposed Al smelter at Aramoana abandoned after public protest
1980s	second proposed Al smelter abandoned again
1985	New trailer suction dredge *New Era* commissioned
1988	Port Companies Act, Harbour Board becomes Port Otago Limited
1989	Region of Otago established
1996–98	Ngai Tahu claim agreement, deed of settlement, Ngai Tahu Claim Settlement Act
1990s	Sewage no longer discharged into Otago Harbour
Mid 1990s	Rock blasting and excavation at Beach Street berth
1993	Clyde Dam on Clutha River (blocking sediment)

2010–11	54 cruise ship calls at Port Chalmers, 8 in Dunedin wharves
2011	Capital dredging for Next Generation Project approved
2016	Customary fishing reserve approved, preventing commercial fishing from Harwood Pt to the mouth of the harbour
2018	Otago Harbour passenger ferry begins service between Portobello and Port Chalmers
2019	First time that over 100 cruise ships visit Dunedin
2020	Replacement of seawalls and development of cycleways begins
2023	Te Aka Ōuākou Dunedin Harbour Cycleway (partially complete) opened
2023–24	Over 120 cruise ships come into Port Chalmers

travelled by the Otago Harbour entrance. Some of that sand was captured by the flood tide, even as it is today. Fortunes made in the goldfields resulted in substantial stone buildings in Dunedin – on land that had once been grassland, wetland, or even harbour.

During this time, shipwrecks at the harbour entrance were surprisingly common, and the harbour itself was beset by shifting sands and shallow drafts (Collins 1995). In 1885 the Otago Harbour Board began work on a mole at Aramoana, cleverly designed to focus water energy through the entrance to keep it open and enable safer shipping. It was completed two years later, to general acclaim. Though it requires regular maintenance, the mole (some 500 m long) and associated dredging keeps the entrance and shipping channel deep and safe for shipping.

Nevertheless, overall, the Harbour was too shallow, so that boats with a draft of more than 2 m could not get to Dunedin. Dredging of channels in Otago Harbour commenced in 1868 with the arrival of the dredger *New Era*, joined in 1877 by the *Vulcan*. Delivery of a third dredger, named *222*, from Scotland in 1882 enabled even more seafloor modification. Dredging was significant: some $5.6 \times 106 m^3$ were excavated during this period (Davis 2009). Dredging, both capital and maintenance, was ongoing from that time, particularly in the Victoria Channel. Blasting and removal of rock began in the 1930s. Even today there are not many days when a dredger is not busy in Otago Harbour.

At the same time, seawalls, jetties, and embankments were being constructed along the shorelines of the harbour. In the 1860s, rock seawalls protected a seaside road from Portobello to Dunedin; by the 1870s a brand new railway line from Port Chalmers to Dunedin was similarly based on an embankment and seawalls. A causeway across Anderson's Bay Inlet was constructed (by prisoners) in the 1860s. Somewhat later a half-tide wall was constructed, over eight km long, to keep sand from drifting into the Victoria Channel. 37 km of 2m-high historic seawalls, carefully rebuilt following development of a new harbourside cycling route, now form the largest Category One Historical Place in New Zealand (Baird 2023).

By the 1900s Otago Harbour was unrecognisable – a rock-wall lined inlet with a deep channel that was fully navigable and with no scrap of wetland or grassy marsh to be seen. A small sandy area remained at Te Raone beach, and a rocky headland at Wellers Rock, but most of the coastline was fully modified. It might seem that the rocky walls would be good habitat for bryozoans and other invertebrates, but they remain surprisingly uninhabited.

Extensive land claim in the Harbour, associated with development of both the city and the port facilities, began in the City of Dunedin area, but have more recently

concentrated on Port Chalmers, providing storage facilities for containers and logs (Davis 2009). In all about 18% of Otago Harbour has been infilled for land claim. At the same time, artificial beaches have been formed by dumping sand from the seaward side of Otago Peninsula, providing recreational amenities in what is mostly a muddy harbour, at Macandrew Bay, Broad Bay, and Deborah Bay. Various reports have noted that the decrease in the tidal compartment caused by land-claim was offset by the increased volume created by dredging.

In 1975–1977, a major dredging project was proposed, and an Environmental Impact Report was required, in which it was noted that dredging would have short-term effects on marine life, but also that consequent changes in hydrology could have longer-term effects. Davis (2009) argued that there was no evidence of damage to the ecology of Otago Harbour, claiming that 'marine plants are widespread and healthy, water quality is good, and birdlife is plentiful.' (Davis 2009, p. 22).

A changing harbour affects the fauna

There is almost no congruence between historical and museum records of Otago Harbour bryozoans and those living in the harbour today. Of the fourteen taxa reported by Hamilton (1897), only *Elzerina binderi* was found in Otago Harbour in 2023, 106 years later. *E. binderi* was reported on two other occasions (Rainer 1981; Davis 2017). Five bryozoan taxa were found both in this study and by Gordon & Mawatari: *Bugula flabellata*, *Calloporina angustipora*, *Antarctothoa bathamae*, *Celleporina proximalis*, and *Watersipora subatra*. *B. flabellata* was documented as being common throughout the harbour by Davis (2017). *Caberea zelandica* was regularly observed between 1955 and 2023 (Batham 1956; Rainer 1981; Table 1). The other bryozoan taxa observed in the past (Gordon 1986; Smith et al. 2010) have either disappeared from Otago Harbour, or were missed in our surveys. Meanwhile we encountered eight additional species hitherto not recorded here.

Many species have disappeared over the last century, perhaps outcompeted by fast-growing exotic bryozoans introduced by shipping (Figure 5). *Watersipora subatra*, *Bugulina flabellata*, and other fast-growing taxa (Smith 2014) were first observed in the inner harbour in 1992 (Gordon and Mawatari), and have been found spreading throughout it since (Morrisey et al. 2007; Davis 2017; Table 3). Such invasive species are typically found in busy ports and other areas of high anthropogenic traffic and disturbance (Davis 2017). Exotic taxa are usually more resistant to anthropogenic stressors and thus may outcompete native taxa. Ongoing shipping presents the opportunity for further invasion events replenishing the populations of invasive taxa.

The most common bryozoan taxa throughout the harbour are currently rapid-growing weedy species, most of which utilise the abundant anthropogenic substrate within the harbour. Piles marking the shipping lane and various buoys provide suitable habitat for encrusting species in an otherwise largely sandy and muddy bottom environment.

Invasive taxa (*Bugulina flabellata* and *Watersipora subatra*) are abundant, with native species such as *Caberea zelandica*, *Celleporina proximalis*, *Calloporina angustipora*, and *Antarctothoa bathamae* limited spatially. Urbanisation appears to encourage the growth of invasive species such as *Watersipora subatra* and *Bugulina flabellata*, both

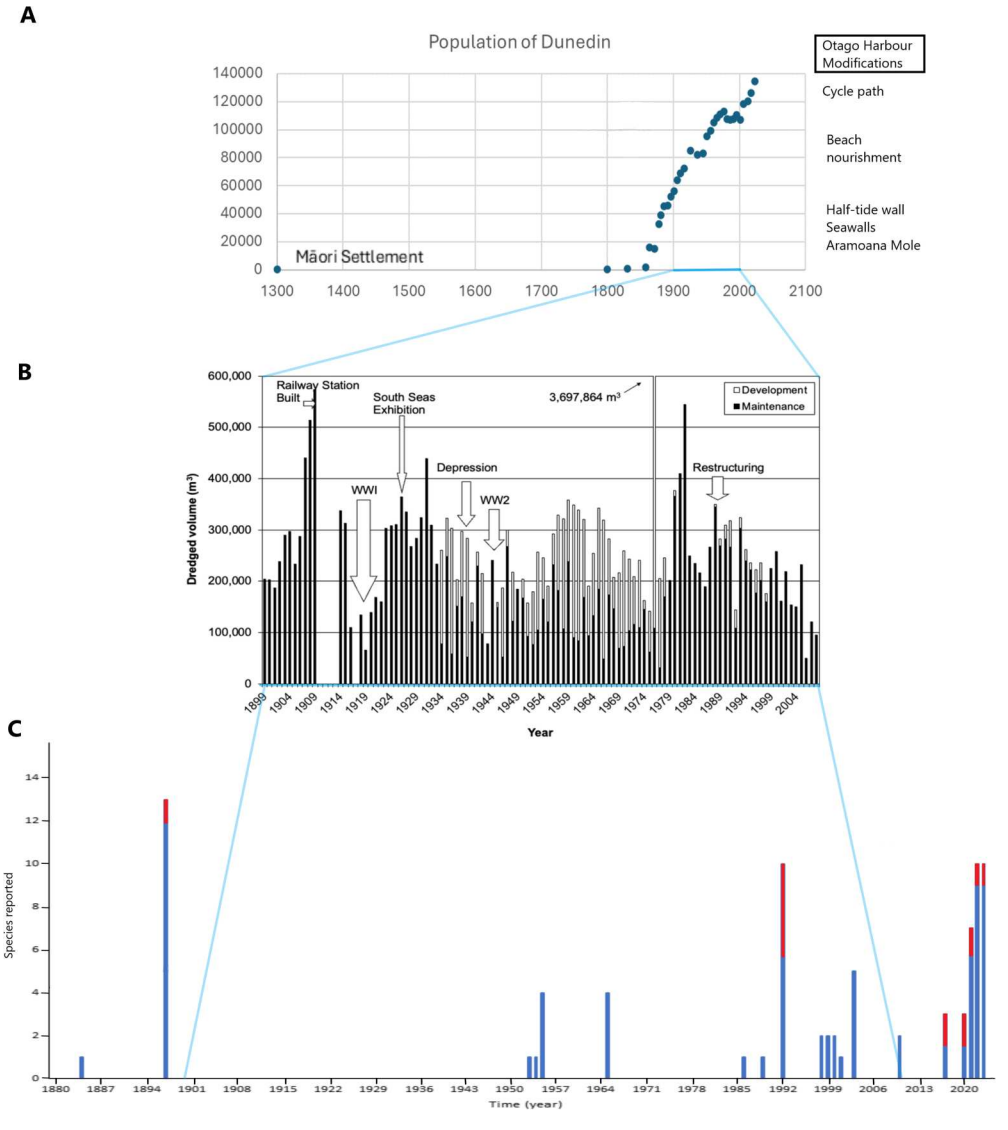

Figure 5. Population of Dunedin from 1300 CE onward **A**, record of dredging in Otago Harbour 1899–2009 **B**, and reported species from recorded bryozoan surveys of Otago Harbour 1884–2023 (blue) with invasive taxa shown in red **C**. Population data was sourced from Thorns & Schrader (2024), and Infometrics (2023).

commonly found in areas with strong anthropogenic influence – Port Chalmers, Portobello, Ravensbourne, Broad Bay, Macandrew Bay, and the city wharves (Davis 2017).

It is striking that, of the ten fouling species Gordon and Mawatari (1992) found in Otago Harbour, four were not re-recorded, meaning they may no longer be present in the Harbour – *Arachnopusia unicornis*, *Chaperiopsis cervicornis, Cryptosula pallasiana*, and S*chizosmittina cinctipora*.

Bryozoans are not the only taxon in Otago Harbour to have had the effect of anthropogenic stressors on them studied (Wells 2018; Babaranti et al. 2018). Sewage pollution

has been found to contaminate mussel beds, and macroalgae at several Dunedin beaches from 2001–2015 (Babaranti et al. 2018).

Additionally, *Austrovenus stutchburyi*, the New Zealand Cockle, has shown evidence of populations within Otago Harbour experiencing a declining growth rate due to modification of the natural environment, with no sites showing an increase in growth rate (Wells 2017).

Shells from sites with the most highly modified areas showed up to a 50% reduction in growth per year, whereas those from the least modifed sites showed no significant changes in growth rate over time (Wells 2017).

When looking more widely at the trends of New Zealand overall, other regions also show a negative effect of urbanisation and anthropogenic stressors on harbour and port ecosystems (MacDiarmid et al. 2012). A 2012 assessment of the threat faced by New Zealand's marine ecosystems found that algal blooms, the benthic accumulation of debris, causeway construction, marine farming, pile moorings, wharves, pontoons, and other construction, have had a moderate to substantial negative effect on harbour ecosystems (intertidal reefs, shell beds, seagrass meadows etc.). Similarly, pollution and invasive species, elevated nitrogen, and phosphorus levels due to pollution, heavy metal contamination, plastic waste, herbicide runoff, pesticide pollution, and increased sedimentation from rivers possess a very high risk to harbour ecosystems (MacDiarmid et al. 2012).

Compared to several other New Zealand ports, Otago Harbour appears to have a high bryozoan diversity – 35 species from 1884 to 2023. Gordon and Mawatari (1992) surveyed ports and harbours around Aotearoa New Zealand and found only a few with more than twelve adventive species (Auckland 22, Napier 13, Nelson 13).

What might have been

An unmodified Otago Harbour would likely look very different from today. Bordered by native forest, abundant in endemic bird-life (Star 1998), the harbour itself would be about 20% smaller in area (not having been filled in during the extensive reclamation of the early twentieth century). While it would be lacking anthropogenic substrates, the harbour shore would include boulders and rocky shore, now almost entirely missing. Without shipping, there would certainly be far fewer exotic bryozoa present, likely none of the fouling taxa that are abundant today. We can assume that water quality and clarity would also be greatly enhanced. The intertidal fauna, as documented by early scientists (Star 1998), would include lush algae, various molluscs and encrusting bryozoans. New Zealand's southern waters are known for their diversity of bryozoans; it is not hard to imagine that an untouched Otago Harbour would have been a hotspot for Bryozoa.

Surveying for conservation

These findings highlight the importance of surveying as a tool for conservation. Without baseline data, there is nothing with which to compare current efforts, or anything to provide an ecological baseline. We know that the number of bryozoan species present in the harbour was previously higher in Otago Harbour than it is today, though

exactly when various species began to disappear and be replaced by exotic taxa is unclear. There are large gaps in the history of Otago Harbour's bryozoan fauna that make finding patterns difficult. Consistent and repeated surveys of a changing ecology and species composition enable conservation and restoration.

While simple distribution data is not exciting, it is the bedrock on which conservation exists. We cannot conserve populations we don't know about; we cannot argue that populations are damaged without a time series of data. Here we have shown that there are several gaps in the records of bryozoan fauna in Otago Harbour, and that more surveys should be performed, but also that the species present have changed over the years.

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Data availability statement

Data are available in Supplementary Data File.

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