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Distribution and current state of freshwater mussel populations (Kāeo, Kākahi) in wadeable Waikato streams

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Abstract

Despite their ecological importance, freshwater mussels (Unionida) are one of the most rapidly declining faunal groups in the world, and New Zealand species are not exempt. New Zealand waterways are home to three mussel species (Hyriidae), which have been classified as 'Data deficient' (*Echyridella onekaka*), 'Threatened-nationally endangered' (*Echyridella aucklandica*) and 'At Risk-declining' (*Echyridella menziesii*) under the New Zealand Threat Classification System. Until recently, research on New Zealand mussel species has been sparse, with large knowledge gaps that still exist, particularly around the distribution and population dynamics of the two *Echyridella* species that co-occur in Waikato streams. To address these knowledge gaps, we conducted widespread freshwater mussel surveys at 120 sites (from 2013 to 2018), across six Waikato sub-catchments using the Waikato Regional Council standardised protocol for monitoring mussels in New Zealand wadeable streams (Catlin et al. 2018), and quantified the abundance, distribution, population size structure, and habitat associations of *E. menziesii* and *E. aucklandica* in Waikato wadeable streams.

Our surveys showed that of the two co-occurring species, *E. menziesii* was the most widespread and abundant, while *E. aucklandica* had limited occurrences in streams across the region. *Echyridella menziesii* occurred at all sites in which live mussel species were detected (63 of 120 sites), while *E. aucklandica* was found only in association with *E. menziesii,* at just 27 of the 120 sites, most of which were in relatively close proximity to the ocean. Mussel densities (no. per m^2) and abundances (no. per 50 m reach), varied across sites and catchments for both species, but were generally lower for *E. aucklandica* (mean $\bar{x}$ = 0.05 per m^2, cf *E. menziesii* at $\bar{x}$ = 0.37 per m^2). Populations in the west coastal Waikato region had the highest densities and abundances of both species, compared to central Waikato streams which had the lowest. Juvenile mussels of both species (<30mm *E. menziesii* and <40mm *E. aucklandica*) were generally sparse, particularly for *E. aucklandica* for which size frequency distributions were skewed towards large individuals at most sites. Low numbers of young mussels, in combination with the low densities of individuals observed for *E. aucklandica* at nearly all sites in which they were found, suggests that most *E. aucklandica* populations are likely experiencing recruitment failure with implications for populations in the near future.

Chemical and sediment pollution, as well as low host fish density, are considered major factors affecting the recruitment of New Zealand mussel species, particularly for *E. aucklandica*, for which common smelt (*Retropinna retropinna*) are at present the only known host. Based on the results of this report, urgent work is required to improve the management and recovery efforts of both mussel species (particularly *E. aucklandica*). As such, we provide, several actionable future recommendations (including habitat restoration, fish passage remediation and outcome monitoring surveys), research opportunities and discuss council's obligations with regard to threatened species under the National Policy Statement for Freshwater Management (2020).

Executive Summary

Freshwater mussels are ecosystem engineers that are increasingly recognised for the many functional roles they play in streams, rivers and lakes, especially where they occur at high densities. Despite their ecological importance, freshwater mussels are one of the most rapidly declining faunal groups in the world, and New Zealand species are not exempt. Declines have been attributed to a wide range of anthropogenic activities including river damming and other habitat modifications, loss of native fish species, introductions of non-native species, as well as toxic pollution and increased nutrient loading. The Waikato region has two species of threatened mussel – *Echyridella menziesii* and the rare *Echyridella aucklandica* – which can occur together in wadeable streams. An understanding of the distribution, abundance, size-frequency associations and habitat requirements of these sedentary, long-lived organisms is important to provide insights into the status of populations across the region and aid in both species' conservation and management. To address this information need, the Waikato Regional Council recently developed a standardised protocol for monitoring mussels in wadeable streams and rivers (see Catlin et al. 2018). Using this protocol, we report here on the results of quantitative mussel surveys from 120 Waikato stream sites across six sub catchments undertaken by the Regional Council in collaboration with the University of Waikato.

Of the 120 sampled sites, mussels were found at 63 sites, with *E. menziesii* detected at all these sites and *E. aucklandica* at 27 sites, always in association with *E. menziesii*. Mussel densities (no. per m^2) and abundances (no. per 50 m reach) varied across sites and catchments but were generally low for both species (*E. menziesii:* mean $\bar{x}$ = 0.37 per m^2; *E. aucklandica* $\bar{x}$ = 0.05 per m^2). *Echyridella aucklandica* was mostly found in coastal sites with connectivity to the ocean, although low density populations were occasionally found in inland Waikato sites. Accordingly, western Waikato coastal streams had the highest densities and abundances of both species. Streambeds across all surveyed sites in which mussels were found, were largely characterised by unconsolidated finer particles (e.g., silt, clay, and sand), with both *Echyridella* species most frequently found within silt substrates.

Sediment and chemical pollution are suspected to be major factors accounting for the decline of juvenile mussels, which are thought to spend part of their early life buried in the substrate. Additionally, low host fish densities appear to be playing a role in affecting the recruitment of New Zealand mussel species particularly for the rare *E. aucklandica*, for which common smelt (*Retropinna retropinna*) are the only currently known host. Evidence of recent recruitment of juvenile mussels (<30mm *E. menziesii* and <40mm *E. aucklandica*) was generally lacking for both species. This was particularly so for *E. aucklandica* populations, for which populations occurred at low densities and size-frequency distributions were skewed toward large mussels at most sites. Skewed population size structures, with low numbers of recent recruits and small mussels, in combination of the low densities of individuals observed for *E. aucklandica* within nearly all sites in which they were found, indicates that possible dramatic decreases in *E. aucklandica* populations in the near future should be a cause for concern.

Based on the results of this report, we urge that appropriate planning and species recovery tools are developed and actioned, particularly for the 'Threatened- nationally endangered' E. aucklandica. As such, we provide a number of actionable future recommendations (including habitat restoration, fish passage remediation, and outcome monitoring surveys), research opportunities and identify council's obligations with regard to threatened species by the National Policy Statement for Freshwater Management (2020).

1 Introduction

Freshwater mussels (Unionida; hereafter 'mussels') are recognised globally for the many functional roles they play, especially when they occur in dense assemblages (i.e., mussel beds of 10-100 individuals per m^2 in streams, rivers and lakes; James, 1985; Spooner et al., 2011; Strayer, 2014; Zieritz et al., 2021). As suspension feeders, mussels have the capacity to remove large amounts of phytoplankton, bacteria, organic and inorganic particles from the water column (Vaughn & Hakenkamp, 2001; Chowdhury et al., 2016; Vaughn, 2018; Zieritz et al., 2019), thereby enhancing not only water clarity, but also the water quality of aquatic ecosystems (Strayer et al., 2008; Atkinson et al., 2013). Mussels also play important roles in nutrient cycling, with their ability to transfer waterborne particles to lake and riverbeds as bio-deposits in the form of egested faeces and non-assimilated pseudofaeces (Vaughn et al., 2007; Collier et al., 2016; Zieritz et al., 2019). Additionally, mussels can increase the abundance and diversity of other benthic invertebrates, by increasing organic matter in sediments and providing stable habitat and refuge through the presence of their shells (Howard & Cuffey, 2006; Spooner & Vaughn, 2006; Allen & Vaughn, 2011). Though historically common on the bottom of many streams, rivers and lakes, mussels are now amongst the world's most imperilled faunal groups (Bogan, 1993; Lopes-Lima et al., 2018). Globally, declines have been attributed to a wide range of anthropogenic activities, which mussels with limited mobility are unable to avoid. Impacts include impoundments and other habitat modifications, introductions of non-native species, as well as toxic pollution and increased nutrient loading (e.g., Strayer & Dudgeon, 2011; Modesto et al., 2018; Moore et al., 2019; Haag, 2019), to which mussel larvae (glochidia) and juveniles are particularly sensitive (Cope et al., 2008; Clearwater et al., 2014). In addition, due to the complex reproductive cycle of mussels, in which glochidia parasitise host fish, and depend on the distribution and abundance of their host to survive (Barnhart et al., 2008), the possible loss of native host fish, is considered a major factor in mussel declines, globally (Haag, 2012).

The slow growth and long lifespans of mussels (from decades to centuries; Grimmond, 1968; James, 1985; Haag & Rypel, 2011) means that populations may be slow to recover from such threats, with surviving adults persisting long after recruitment of young mussels has slowed or stopped. Such relict populations of aging adults are commonly reported (e.g., Geist & Auerswald, 2007, Österling et al., 2010), and may represent "extinction debts" (future extinction of species owing to past events; Tilman et al., 1994), that will only become apparent over time, after these long-lived mussels eventually die out (Strayer et al., 2004; Vaughn, 2012). In New Zealand, streams, rivers and lakes are home to three endemic extant mussel species (known as kāeo, kākahi and torewai). Mussels, here, are recognised as culturally important taonga for tangata whenua, given their use as traditional tools and food sources (mahinga kai; Garibaldi & Turner, 2004; Hiroa, 1921). The three New Zealand species comprise the naturally uncommon *Echyridella onekaka*, which has a restricted range in north-west Nelson, as well as the widely distributed *Echyridella menziesii*, which exists throughout New Zealand's North and South Islands, and is often found together within Waikato streams with the rare *Echyridella aucklandica* (Gray, 1843; Fenwick & Marshall, 2006). Like many mussel species across the globe, New Zealand mussels are declining, with the two species present within the Waikato region, *E. menziesii* and *E. aucklandica*, classified as 'At risk – Declining' (*E. menziesii*) and 'Threatened – Nationally Endangered' (*E. aucklandica*) according to the New Zealand Threat Classification System (Grainger et al., 2018). Previous research on the basic biology of New Zealand mussels has been sparse, with the main focus of studies on *E. menziesii* populations, mostly in lakes (e.g., Phillips, 2007; Phillips et al., 2007; McEwan, 2015; Collier et al., 2016; Cyr et al., 2017; Roper & Hickey, 1994). More recently, though, knowledge gaps on the biology and ecology of Waikato stream dwelling *E. aucklandica* and *E. menziesii* have been addressed, including data on diet overlap, reproduction and phenology, host fish associations, and movement of both species (Hanrahan, 2019; Melchior et al., 2019; Collier & Melchior, 2020; Melchior et al., 2021; Melchior, 2021). Information gaps still remain regarding the distribution, population size structure, and habitat requirements of both species, particularly for *E. aucklandica*. Thus, the specific aims of the surveys reported here were to establish a baseline understanding of abundance and distribution, including population size structure estimates, and reach-scale habitat associations of both *E. menziesii* and *E. aucklandica* in Waikato wadeable streams using standardised protocols outlined by Catlin et al. (2018). This report provides an initial data set that may contribute to long-term monitoring of population density and size-structure changes over time and enable comparisons with other regions across New Zealand. Based on the results of this report, we provide several actionable future recommendations and research opportunities to improve the management and recovery efforts of both mussel species.

2 Method Overview

Mussel surveys were undertaken using Protocol 3 in Catlin et al. (2018). An important goal was to expand the known spatial distribution of mussel species in flowing environments from those published in Marshall et al. (2014). Consequently, survey site selection was intended to achieve spatial coverage across both regional and catchment scales, and incorporate a range of stream typologies (e.g., inland and coastal, steep and low gradient, small and larger sites). Sites were initially screened using GIS to select potentially accessible sites. Once on-site, a suitable wadeable reach was selected (see section 2.1 for details and Figure 4 for sampling site locations). A total of 120 sites were surveyed across the region. Seventy-nine of these sites were assessed for mussel populations by the Waikato Regional Council during base flow conditions, in March to May over 2013-2018. These sites were spread across five sub-catchments within Waikato Region, covering Raglan Harbour, Upper West Coast, Kawhia and Aotea Harbours, Waipā and Hauraki; Figure 4). The University of Waikato surveyed 41 sites in the lower Waikato and Waipā catchments from November to January in 2015/16 (Melchior & Neijenhuis unpublished data; Neijenhuis, 2015). Specific site coordinates are not published in this report (as per the recommendations of Rainforth (2008)). All data in this report are archived at the Waikato Regional Council.

If at a given site, a heavy rain event occurred, surveys were delayed for at least two weeks to ensure safe wadeability (low water levels and flow conditions) and sufficient water clarity or visibility. The low number of surveyed sites in the Hauraki catchment is partly a result of weather events leading to delays during the available survey window, whereas within the lower Waikato catchment it was due to persistent poor clarity. Multiple parameters were recorded to represent mussel populations at the reach scale of each site, while at the same time individual mussel attributes were also collected. Here, the objective was to collect a wide range of data throughout each survey reach to identify environmental parameters associated with mussel presence and habitat characteristics affecting abundance.

2.1 Mussel survey methodology

2.1.1 Presence/absence surveys

Surveyors undertook an initial visual survey of up to 30 minutes total surveyor effort (e.g., where two people were present 2 x 15 = 30 minutes) using bathyscopes and targeting likely mussel habitats (e.g., along banks/ undercuts/ macrophytes/ shaded areas/ logs) to determine their presence or absence (Figure 1a, b). GPS readings and photographs at the survey start and finish locations were taken for all sites, and physicochemical parameters recorded (see Section 2.1.3). Prior to leaving a site, all of the equipment used, including waders and measuring tapes, was decontaminated using suitable disinfectant.

Figure 1. Surveyors undertake mussel surveys using bathyscopes in Waikato streams (A, B). Length measurements taken of the valves of *Echyridella menziesii* (C) and *E. aucklandica* (D) using callipers.

2.1.2 Population surveys

If mussels were found during the initial presence/absence survey, an additional population survey was commenced proceeding for 50 m upstream of the location of the first mussel detected. The stream reach was divided into five sub-reaches of 10 m and the wetted width (m) and thalweg depth (m) were measured at the start of each sub-reach. Following this, intensive hand and visual searches for mussels were conducted in all habitats across each sub-reach. When a mussel was found, it was gently lifted from the substrate and a tactile search was undertaken one hand-width away from where the mussel was found, to detect any other buried mussels nearby.

The first 50 individuals of each species were measured (except some sites within Kawhia and Raglan catchments, where more individuals were measured) and assessed for condition, after which only a count was recorded of each species (see protocol 3 by Catlin et al., 2018). Length (maximum measure along the anterior-posterior axis), height (maximum dorso-ventral axis, not measured through umbo) and width (maximum lateral axis) were measured (to the nearest mm) using Vernier callipers (Figure 2). The condition or erosion of each individual (i.e., how worn the shell is, categorised into five sub-categories, 0%, 1-25%, 25-50%, 50-75% and 75-100% see Section 3.3) was determined following Roper and Hickey 1994. Habitat characteristics were recorded for each mussel measured (see Section 2.1.3).

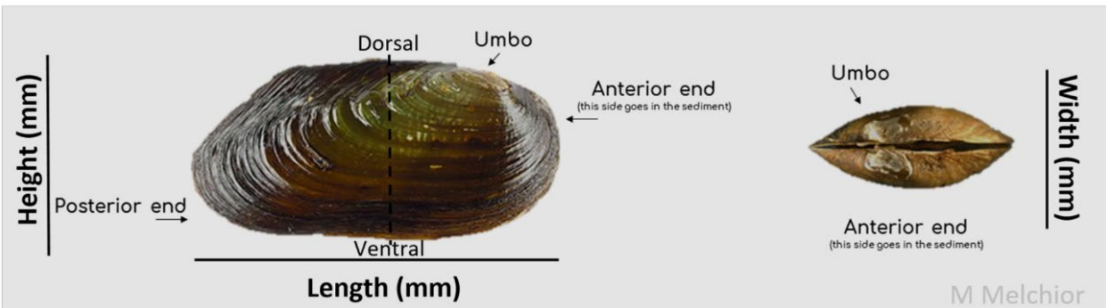


Figure 2. Biometric parameters length, height and width (mm) of mussels measured in this report. The species shown is *Echyridella aucklandica*.

2.1.3 Habitat assessment

Habitat parameters assessed for each measured mussel (see above) were based on Catlin et al. (2018) and included: microhabitat type (macrophyte, wood, bank foot, undercut, root mat or sand bar), substrate type percentage (clay, silt, sand, small gravel, large gravel, cobble, boulder, bedrock), position across channel divided into thirds (true left, middle, true right), channel morphology (outside bend, straight, inside bend), and flow habitat (run, riffle, pool, backwater). Any dead mussel shells that were found within the stream or on the banks were also recorded if both valves of the shell were present. Reach scale habitat assessments for the 50 m survey reach were based on Collier and Kelly (2005) and Clapcott (2015).

2.1.4 Physicochemical measurements

Spot water quality measurements of temperature (˚C), dissolved oxygen (DO%, DO mg L^{-1}) and specific conductivity (µS/cm; HACH HQ30D meter, Loveland, Colorado, USA) were taken. Substrate compaction categories and fine substrate embeddedness categories were identified for each reach (compactness categories include I = No packing, easily moved, II = Mostly a loose assortment with little overlap, III = Moderately packed with some overlap, IV = Assorted sizes, tightly packed and/or overlapping; fine particle embeddedness categories: 0%, 1-25%, 25-50% and 75-100%. Additionally, water samples were collected from all sites, excluding those surveyed by the University of Waikato, and stored on ice for analysis of physicochemical parameters at the accredited Hill Laboratories. Water hardness and pH were assessed to identify their potential effects on mussel valves, while metals were analysed to identify potential impacts on juvenile mussels, as outlined by Clearwater et al. (2014). Last, we assessed nutrients to identify any impacts of the surrounding land use (see Catlin et al. 2018 for full list of parameters).

2.1.5 Data analysis

All data were assessed for normality (Kolmogorov-Smirnov test and Q-Q plots) and homogeneity of variances (Levene's test). Where parametric assumptions could not be confirmed, non-parametric tests were used. Statistical significance for all tests was defined at $p = 0.05$. To assess the distribution and abundance of mussels across the Waikato region, both species abundances (no. per 50 m length) and densities (no. per m^2) were calculated for each site. Densities were calculated by dividing number of mussels by the area surveyed. Mussel densities (no. per m^2) were adjusted to account for any area unsearched (e.g., high water depths), while mussel abundance (no. per 50 m reach) did not account for identified unsearched areas.

Five density/abundance categories were identified according to the overall distribution of quartiles of data pooled for each species (based on Hastie et al., 2000), as follows: 'E' or 'Locally Absent'; 'D' or 'Locally Rare' (up to the first quartile), 'C' or 'Locally Occasional' (between the first and second quartiles), 'B' or 'Locally Frequent' (between the second and third quartile), and 'A' or 'Locally Common' (above the third quartile). Both abundance and density data were considered when assigning these classifications. To validate the use of abundance data (no. per 50 m length) for the classifications and rule out an effect of stream width (m) on number of individuals present per 50 m reach length, Spearman correlation matrices were carried out, which identified no correlation between abundance and stream width for both species (*E. menziesii*: r 0.14, $p = 0.3$; *E. aucklandica*: r 0.20, $p = 0.32$, Figure 3). Visual interpretations of density bands for each species across the six catchments surveyed, were created through density/abundance maps derived using ArcGIS pro 3.0 (2021). Different diameters of circles were divided into each density band proportional to the value of density categories.

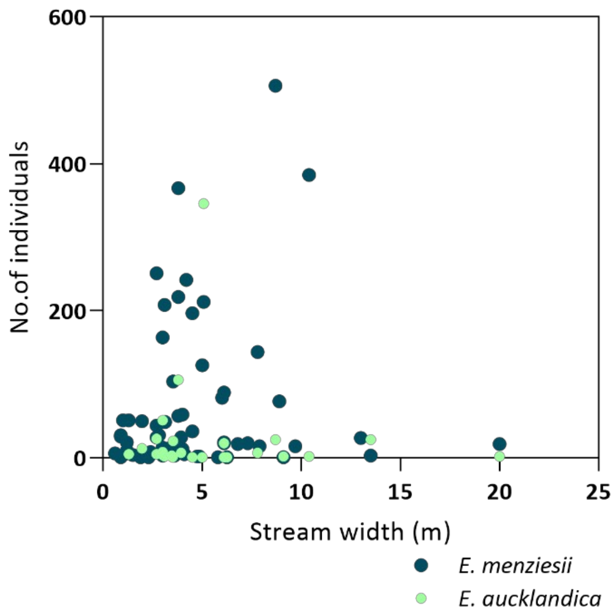


Figure 3. Correlation between number of individuals of each species (*Echyridella menziesii* and *E. aucklandica* per site, i.e., 50 m reach) and stream width.

Recruitment to a population was considered to be occurring when individuals of <30mm length were recorded for *E. menziesii* and <40 mm for *E. aucklandica*. Recruitment considerations were based on i) age to length calculations for *E. menziesii*, with mussels <30 mm having been reported to be younger than two years (James, 1985; Rainforth, 2008), and ii) on length at sexual maturity estimations for both species by Melchior (2021). Two-sample Kolmogorov-Smirnov (K-S) tests were performed to compare univariate distributions of *E. menziesii* and *E. aucklandica* population size structures (shell length) across catchments. Kruskal-Wallis (K-W) tests were carried out to determine differences in shell morphometry (shell length and length: height ratio) for each species between catchments, followed by Dunn's post-hoc multiple comparison tests with Bonferroni correction.

Water quality parameters were assessed for statistically significant differences between sites in which mussels were present, and sites in which they were absent using a Mann Whitney *U* test, while Kruskal-Wallis tests (followed by Dunn's post-hoc multiple comparison tests with Bonferroni correction) were calculated to compare water quality parameters between catchments.

3 Results

3.1 Mussel distribution and abundance

3.1.1 Distribution

Mussels occurred at 63 of the 120 (53%) sites surveyed, being present within each of the six sub-catchments sampled. *Echyridella menziesii* was more widely distributed than *Echyridella aucklandica*, occurring at all 63 sites in which mussels were present. Individuals of *E. aucklandica* only occurred in association with *E. menziesii* and were found at only 27 of the surveyed sites, while 36 sites were exclusively populated by *E. menziesii* (Table 1). The only sub-catchment in which *E. aucklandica* populations were not found, was the lower Waikato catchment (Figure 4).

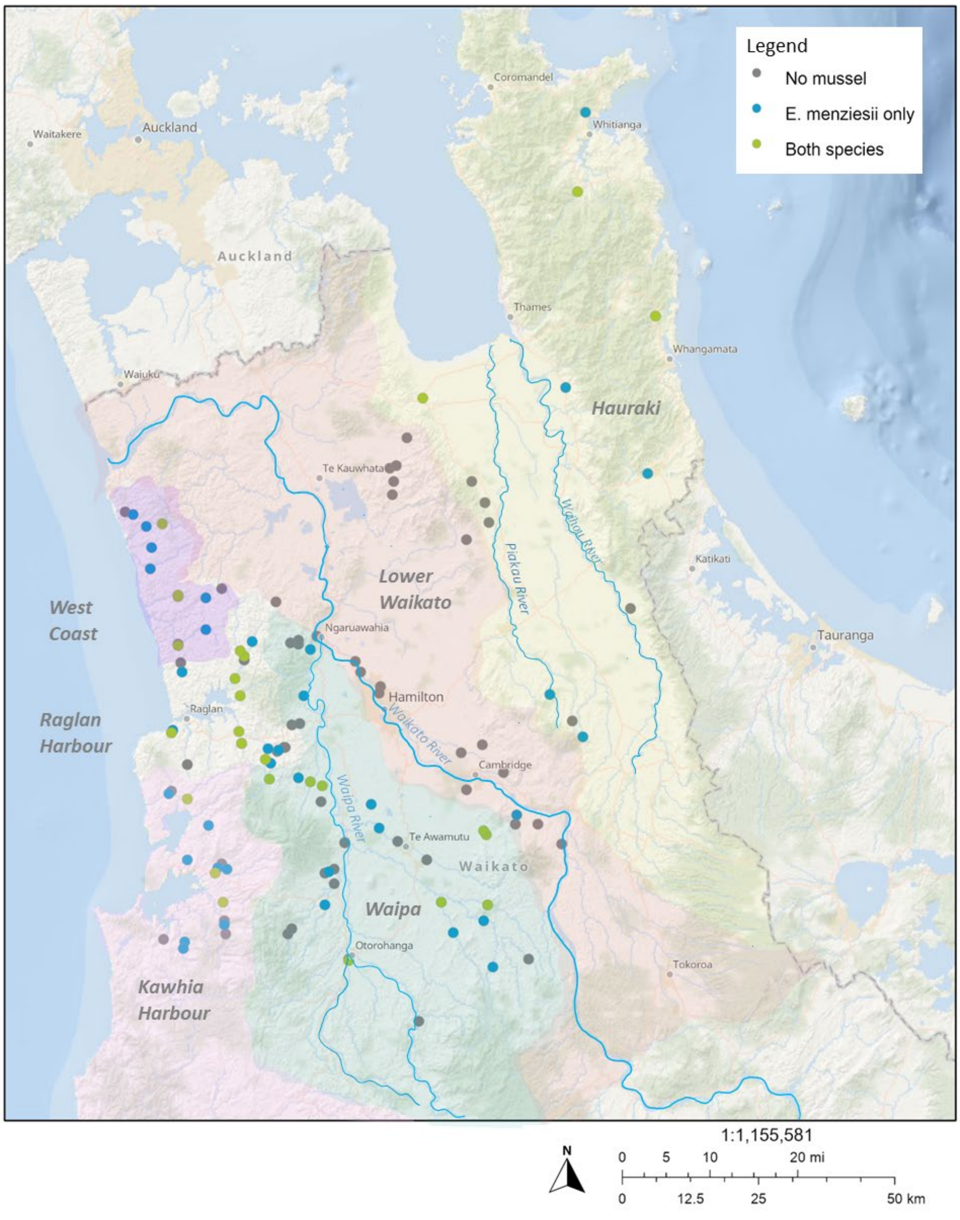


Figure 4. Mussel monitoring sites surveyed across six catchments within the Waikato region. Points indicate sites in which mussels were absent (grey), only *Echyridella menziesii* were present (blue) and both *E. menziesii* and *E. aucklandica* were present (green).

Of the six catchments surveyed, Waipā and Raglan Harbour comprised the greatest proportion of sites in which mussels occurred. Raglan Harbour contained the highest proportion of *E.*

aucklandica sites, while Waipā contained the highest proportion of sites with *E. menziesii*, although it is important to note that this was also the catchment in which the greatest sampling effort occurred (n = 39 total sites visited). The catchment with the lowest number of sites in which mussels were found was the lower Waikato, where only two of the 20 surveyed sites detected only *E. menziesii* populations (Table 1).

Table 1. Breakdown of number of surveyed sites in which mussels were either present or absent within each catchment (percentages in parentheses)

Catchment	Sites with mussels present	Sites with *E. menziesii only*	Sites including *E. aucklandica*	Sites with no mussels present	Total visited sites
Hauraki	8 (67%)	5 (42%)	3 (25%)	4 (33%)	12
Kawhia	11 (61%)	8 (44%)	3 (17%)	7 (39%)	18
Raglan	16 (89%)	6 (33%)	9 (56%)	2 (11%)	18
Waipā	17 (44%)	9 (23%)	8 (21%)	22 (56%)	39
West Coast	9 (69%)	6 (46%)	3 (23%)	4 (31%)	13
Lower Waikato	2 (10%)	2 (10%)	0 (0%)	18 (90%)	20
Total	**63 (53%)**	**36 (30%)**	**27 (23%)**	**57 (48%)**	**120**

3.1.2 Mussel abundance

A total of 4902 mussels were recorded from the sampling sites across the Waikato region with abundances varying between sites and catchments (Figure 5). *Echyridella menziesii* was the most abundant species, accounting for 86% (n = 4213) of the total number collected, while *E. aucklandica* accounted for 14% of mussels (n = 689). When analysing abundances per site (50 m reach) at locations at which mussels were present, across the surveyed catchments *E. menziesii* was found with mean (± SE) abundances of 67 ± 105 mussels per 50 m reach (min = 1, max = 506) while *E. aucklandica* averaged 26 ± 68 mussels per 50 m reach (min = 1, max = 346). Kawhia Harbour sites had the greatest *E. menziesii* average abundances, while the Raglan catchment sites yielded the greatest average abundances of *E. aucklandica* (Figure 5). Although the Waipā catchment had the highest number of sites supporting mussels (Table 1), this catchment, along with the Lower Waikato catchment had the lowest mussel abundances (Figure 5). Sites in which both species were present were generally dominated by *E. menziesii* across all catchments, however, for some sites within the Raglan (Ohautira, Waingaro) and Kawhia (Te Kauri) catchments, *E. aucklandica* was the most abundant or equally prevalent species (Figure 6).

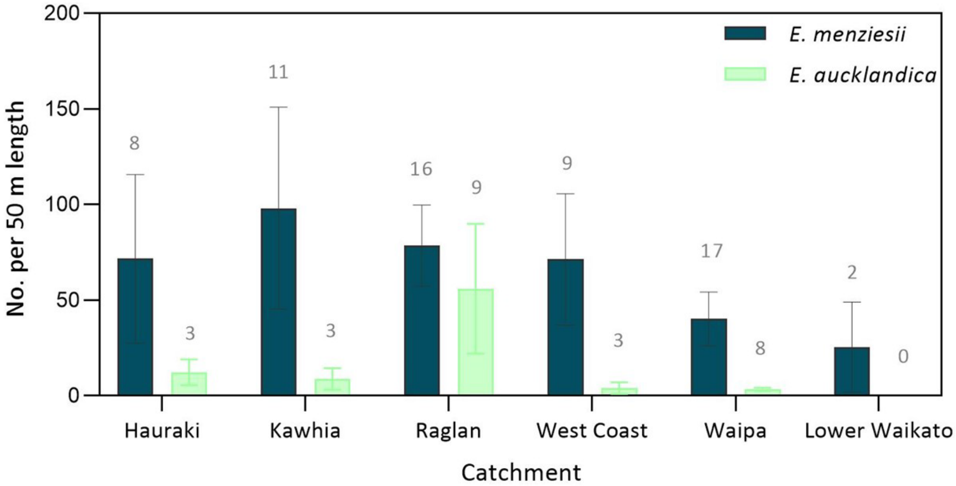


Figure 5. Mean abundances (± SE) of *Echyridella menziesii* and *E. aucklandica* (no. per 50 m) at sites in which mussels were present within the six catchments. Number of sites sampled is annotated above each catchment in grey.

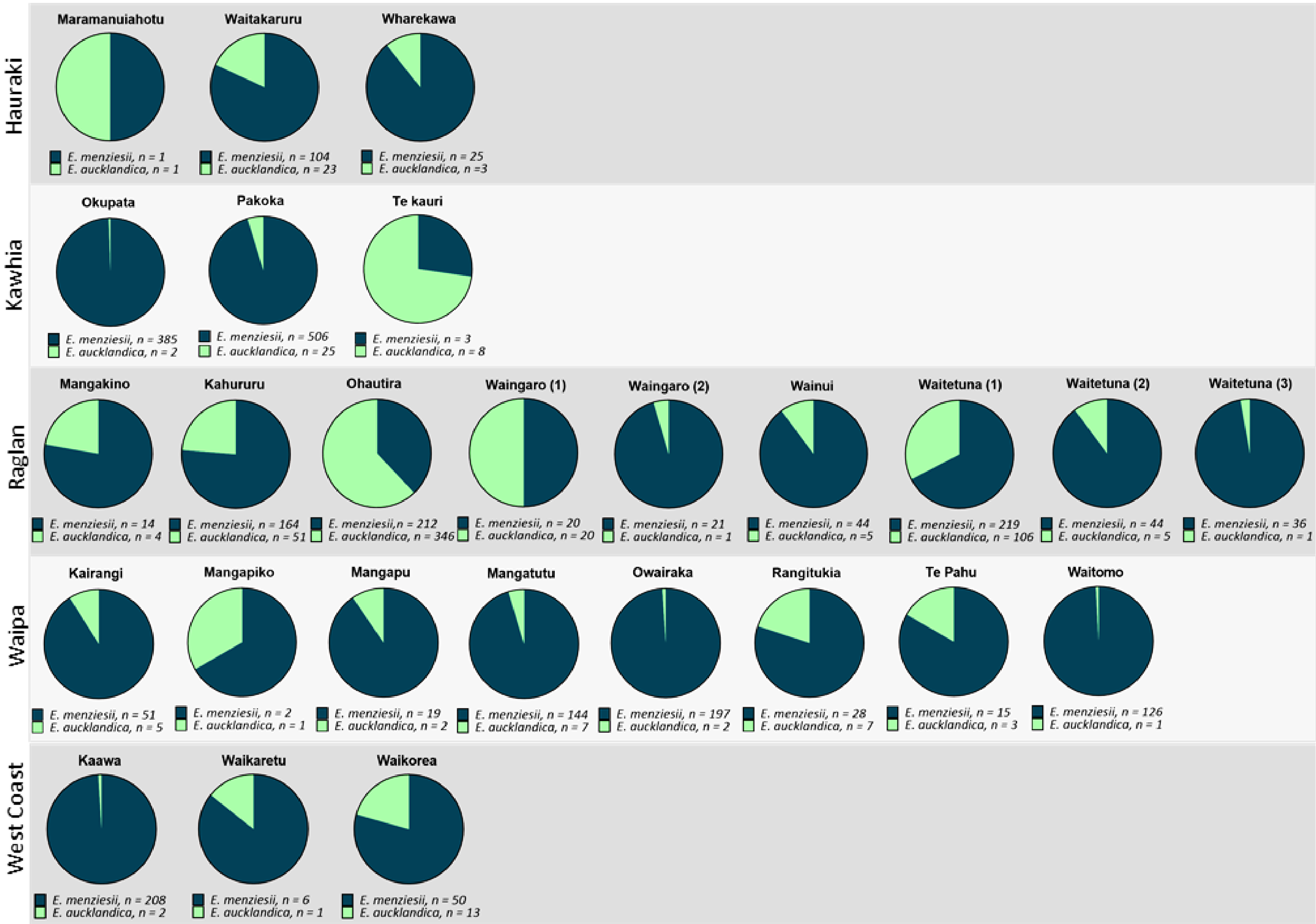


Figure 6. Relative abundance of *Echyridella menziesii* and *E. aucklandica* found within sites that contained both species within each catchment.

3.1.3 Mussel densities

Across surveyed sites, mussel densities were generally <1 mussel per m^2. *Echyridella aucklandica* were found at particularly low densities ($\bar{x}$= 0.05 mussels per m^2, min = 0.003; max = 1.38), with only one site where the populations density was >1 per m^2 (Ohautira, Raglan). *Echyridella menziesii* densities were variable among sites, averaging 0.37 mussels per m^2, with minimum density where they occurred of 0.03 per m^2 and maximum density of 1.9 mussels per m^2. The highest mean densities for *E. aucklandica* were found at sites flowing into Raglan Harbour, while West Coast catchments had the highest average densities of *E. menziesii* (0.55 mussels per m^2; Figure 7), largely driven by a population found within the Kaawa Stream. The lowest densities for *E. menziesii* were found in the Waipā and Lower Waikato catchments (Figure 7).

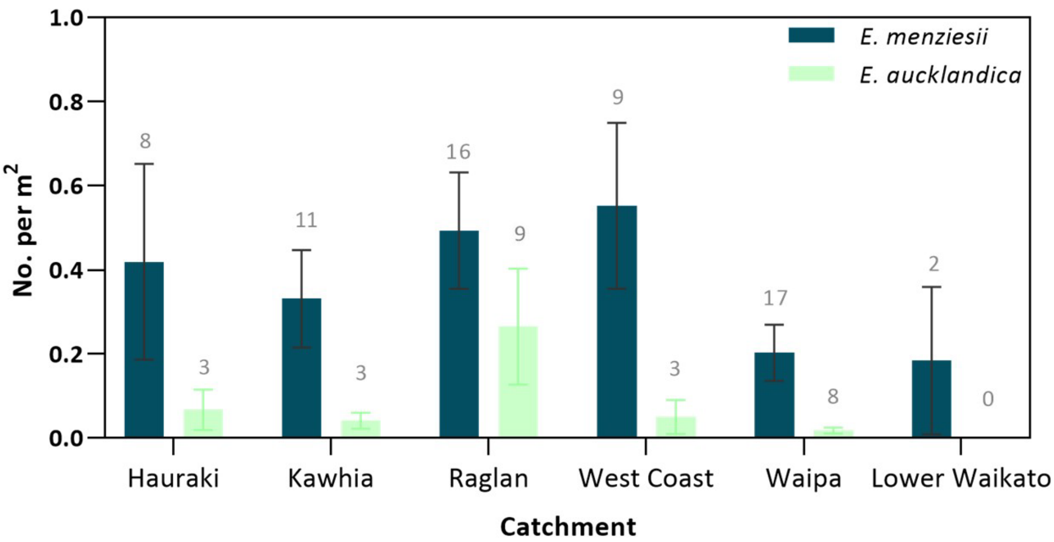


Figure 7. Mean densities (±SE) of *Echyridella menziesii* and *E. aucklandica* (individuals per m^2) at sites in which mussels were present within the six catchments. Number of sites sampled are annotated above each catchment in grey.

3.1.4 Density classifications for mussel populations

Five proposed density/abundance classification categories (A = 'Locally Common' >80 *E. menziesii* per 50 m reach, >25 *E. aucklandica* per 50 m reach to E = 'Locally Absent', see Table 2; Figure 8) were identified according to the overall distribution of quartiles of abundance data (number per 50 m length) and density (no. per m^2) pooled for each species (Table 2). To aid interpretation, abundance data (no. per 50 m length) was included in these classifications due to the very low areal densities found for both species throughout most surveyed sites. This also helped to account for most mussels being associated with bank habitats regardless of river or stream width. The bands are proposed for use as a comparative baseline for similar streams and rivers across the Waikato Region. Taking the proposed density bands into account (Table 2; Figure 8), most *E. menziesii* sites were classified as 'Locally Occasional' while sites with *E. aucklandica* were spread evenly across all categories ('Locally Common' to 'Locally Rare' excluding the category 'Locally Absent' which contained the highest number of sites due to the low occurrences of *E. aucklandica* across the Waikato region (Figure 8).

Table 2. Proposed density classifications for current mussel abundances (mussels per 50 m length) and densities (mussels per m^2) of the two species *Echyridella menziesii* and *E. aucklandica* across in the Waikato region.

Density category	Terminology	*E. menziesii* per 50 m length	*E. menziesii* per m^2	*E. aucklandica* per 50 m length	*E. aucklandica* per m^2
E	Locally Absent	0	0	0	0
D	Locally Rare	<5	<0.005	<1	<0.007
C	Locally Occasional	6-19	0.006- 0.15	2-4	0.008-0.03
B	Locally Frequent	20-79	0.16-0.6	5-24	0.04-0.1
A	Locally Common	>80	>0.7	>25	>0.2

Sites classified into the highest density bands (A; 'Locally common' - B 'Locally Frequent') for *E. aucklandica* were more prevalent in coastal areas, with particular clusters of high-density populations around the Raglan Harbour, while central, inland sites containing *E. aucklandica* were categorised as having 'Locally Occasional' (C) and 'Locally Rare' (D) local populations (Figure 8a). *Echyridella menziesii* sites considered within the higher classifications were distributed throughout the region, occurring in both coastal and inland sites (Figure 8a,b). Many inland surveys show sites with the classification 'E', indicating an absence of either species. As shown in the maps, future sampling effort could be directed towards lowland tributaries of the lower Waikato and waterways in the northeast of the Waikato region (Hauraki, Coromandel; Figure 8 a,b).

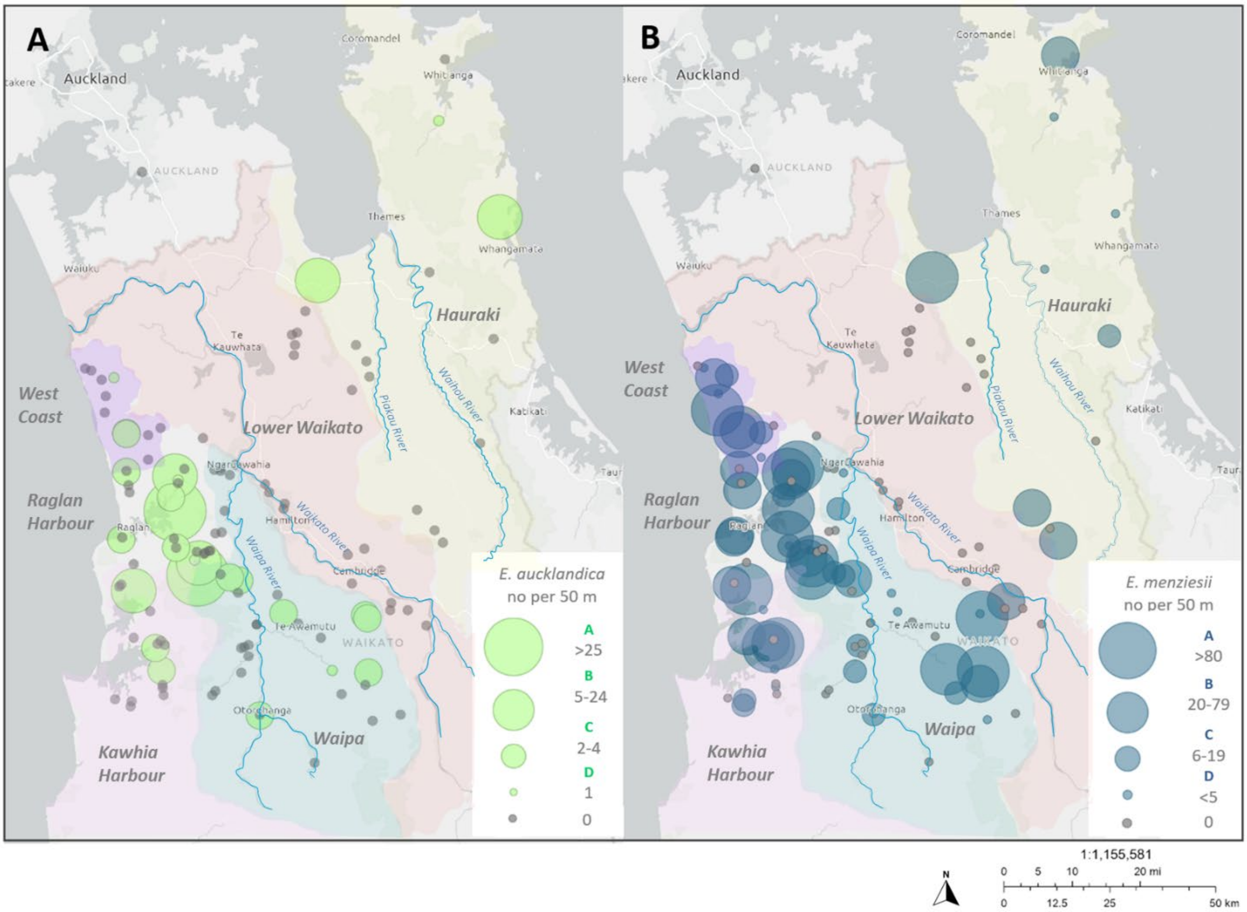


Figure 8. Maps showing *Echyridella aucklandica* (A) and *E. menziesii* (B) densities (individuals per 50 m length) across the six catchments, categorised into species specific density bands (A, B, C, D; see legend) for each site across all survey catchments. Diameter of circles are proportional to the value of density categories. Black circles differentiate from coloured circles to show sites in which mussels were absent (density = 0).

3.1.5 In-stream mussel detection

A greater proportion of individuals of both species were found fully or partially emergent, protruding through the substrate (*E. menziesii* 75%; *E. aucklandica*: 92%) rather than completely buried (*E. menziesii*: 18%; *E. aucklandica*: 3.5%) (Table 3). For *E. menziesii*, this equated to a ratio of 4:1 emergent to buried mussels, while for *E. aucklandica* the ratio was 26:1. These proportions paralleled the search methods that were utilised, where a greater proportion of mussels were detected by visual searches compared to tactile searches. Accordingly, 75% of 1409 *E. menziesii* were found visually with the remainder found by tactile searching through the substrate, while almost all 366 *E. aucklandica* (92%) were found visually (Table 3). Thus, if visual searches only were to be undertaken, it is likely that 25-30% for *E. menziesii* and 6-8% for *E. aucklandica* would need to be added to population estimates.

Table 3. Mussel numbers and percentages (%) that were found emergent or buried and their respective search method for all sites where mussels were found (excluding University of Waikato data).

	E. menziesii		***E. aucklandica***	
Emergence*	**n**	**%**	**n**	**%**
Emergent	1426	**75**	337	**92**
Buried	334	18	13	4
Unrecorded	128	7	16	4
Total assessed	1888		366	
Search method*				
Visual	989	**70**	183	**94**
Tactile search	420	30	10	6
Total assessed	1409		193*	

NB* Lower number of total mussels assessed for emergence and search method, as these parameters did not get introduced until the 2014 survey season, and exclude University of Waikato data.

3.2 Population size structure

Length-frequency relationships across all sites where mussels were present were unimodal for both species. *Echyridella menziesii* shell length profiles across all sub-catchments were relatively normally distributed, with mussels found at median shell lengths of 57 mm, ranging from 19 mm to 95 mm. *Echyridella aucklandica* was found with mostly skewed size-distributions that deviated from normality with a narrower range of lengths recorded across all catchments (36 mm to 112 mm, median 89 mm; Figure 9). Median shell lengths varied significantly between catchments for both species (*E. aucklandica*: K-W: n = 693, H = 114.2, p <0.001; *E. menziesii*: n = 3866, H = 401.3, p<0.001). For *E. aucklandica*, the most significant pairwise length differences occurred between catchments Hauraki and Waipā where lengths were smallest, versus Kawhia and Raglan where *E. aucklandica* were largest (Figure 9; Appendix 1). For *E. menziesii*, significant size differences were found between all catchments, except between Hauraki and Waipā, and between Raglan and the West Coast (Figure 9; Appendix 1). The largest *E. menziesii* individuals (>90 mm) were found within the Raglan and Waipā catchments (Figure 9; Appendix 1). Across all sites, 0.5% of *E. menziesii* shells measured (n = 21 of 3866) were categorised as recent recruits or juveniles (i.e., ≤ 30 mm, Rainforth, 2008; Melchior, 2021), with juveniles evident at only 12 of the 63 sites and 4 of the 6 sub-catchments Figure 9). For *E. aucklandica* the number of detected recent recruits or juveniles was even lower, with only 2 juvenile mussels of 693 sampled *E. aucklandica* individuals (juveniles ≤ 40 mm, Melchior, 2021) detected across catchments, suggesting that recruitment was evident at only 2 of the 27 sites in which *E. aucklandica* was found (i.e., Raglan harbour).

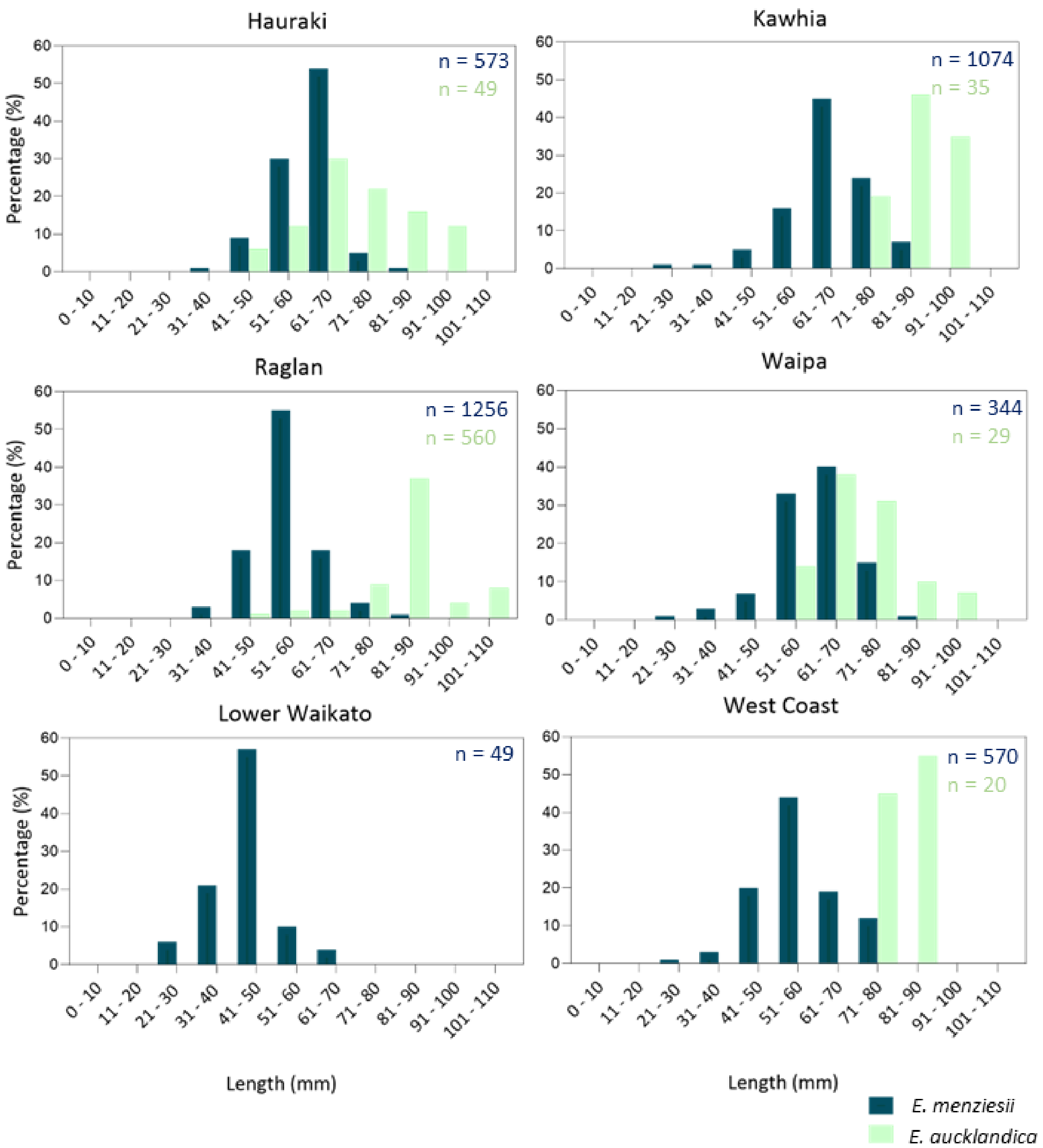


Figure 9. Length frequency distributions (% of total numbers) for *Echyridella menziesii*, and *E. aucklandica* valves from all surveyed streams in which mussels were present within each catchment. Total number of each species is given within each plot (blue = *E. menziesii*, green = *E. aucklandica*).

3.3 Shell characteristics

The morphometry of *E. menziesii* shells can be described as sub-elliptical (due to their rounded anterior and posterior margins). *Echyridella aucklandica*'s shell morphometry, on the other hand, can generally be described as sub-trapezoidal, due to their length being greater than their height (Figure 10). *Echyridella menziesii* sub-elliptical shell shapes were generally found with length: height ratios of 1.7, between 1.5-2.0, while *E. aucklandica* shells, generally had length: height ratios of >2.0 (Figure 10b). Across the catchments, length: height ratios significantly varied in both species (*E. aucklandica*: K-W: n = 693, H = 22.5, p <0.002; *E. menziesii*: n = 3866, H = 101.1, p <0.001). Though found to be significantly different, *E. aucklandica* shell shapes (length: height ratios) generally showed low variability between catchments, with the only catchments in which shell shapes were found to be significantly different, were between the Raglan (with greater mean length: height ratios of 2.2) and Waipā catchments (lowest mean length: height ratios of 2.0 p <0.0003; Figure 10b). In comparison, *E. menziesii* shell shapes were more variable across the region, with significant differences across all catchments, except between Hauraki and Raglan (p

= 0.2), Waipā (p = 0.9) and the West Coast (p = 0.2), and between populations within the Waipā and West coast (p = 0.1) (Figure 10a; Appendix 2). Length: height (L:H) outliers, particularly above 2.5 (L:H) for *E. menziesii* seen in the Raglan and Waipā catchment box plots may indicate measurement errors, or potential misidentification of species (Figure 10a).

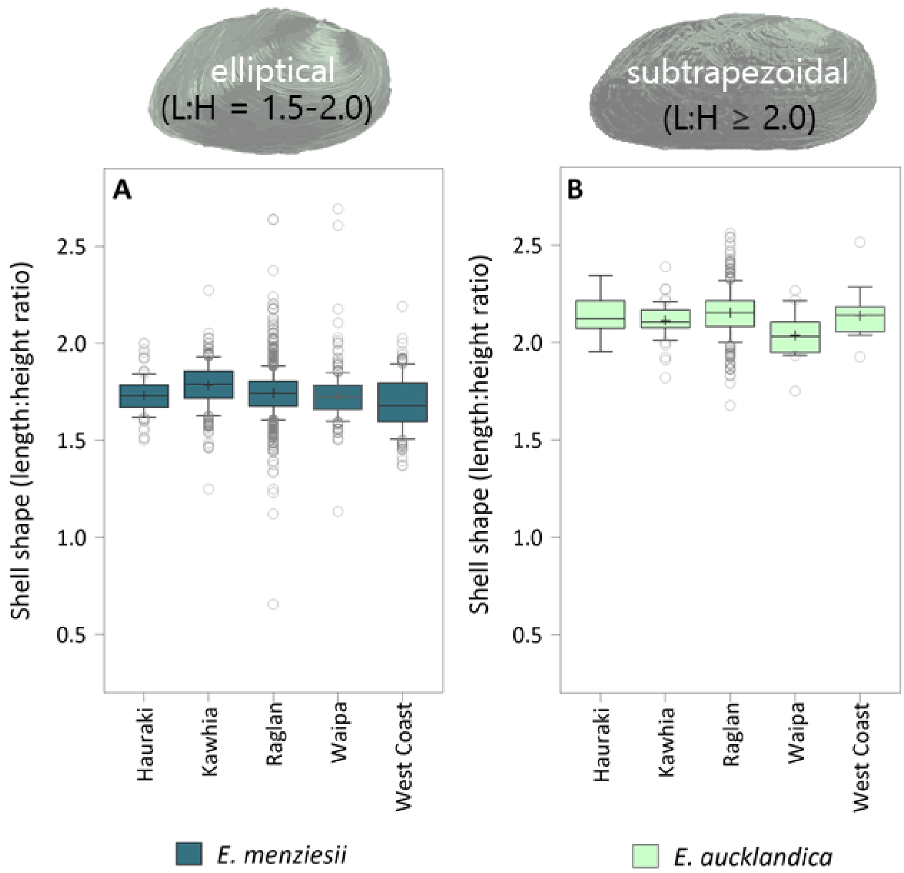


Figure 10. Shell shape length: height ratio boxplots for *Echyridella menziesii* (A) and *E. aucklandica* (B) across catchments. Box boundaries indicate interquartile ranges; within each box are the mean (+), whiskers are 10th and 90th percentile, while outer circles denote outliers. Length:height ratios for *E. menziesii* and *E. aucklandica* based on North American species following Nedeau et al., 2009.

Shells were generally found to have similar patterns of shell erosion, with the lower categories of erosion dominant in both species. For example, 78% of 1834 *E. menziesii* and 80 % of 555 *E. aucklandica were* assessed as having erosion levels between 1-25% (erosion category II), followed by the more moderate erosion level category III (25-50%) in which 15% *E. menziesii* and 14% *E. aucklandica* of assessed individuals were affected. Across all sites, both species showed little evidence of heavy erosion (*E. menziesii*: 2%; and *E. aucklandica*: 3%; Figure 11).

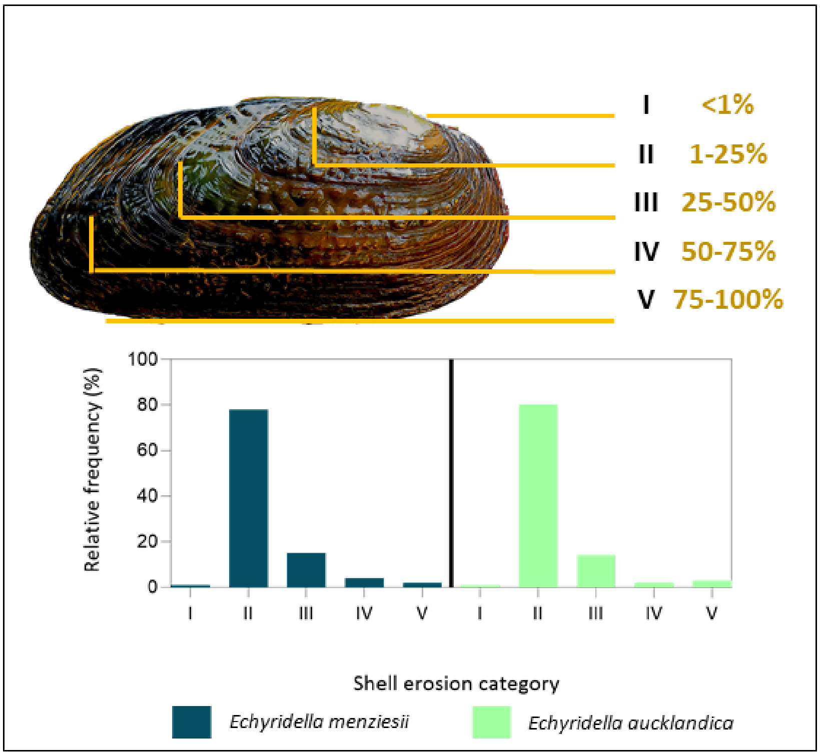


Figure 11. Relative frequency distributions (%) of *Echyridella menziesii* (n = 1834) and *E. aucklandica* (n = 555) across all catchments assessed for shell erosion (erosion categories modified from Roper & Hickey (1994). See Appendix 3 for details.

3.4 Habitat characterisation

3.4.1 Reach characteristics

Pasture was the most dominant vegetation type alongside reaches across all sites with and without mussels, making up 70% of all sites containing *E. menziesii* and 82% of sites containing *E. aucklandica* (Table 4). Most sites in which *E. menziesii* and *E. aucklandica* occurred were partly shaded (*E. menziesii*: 60% shade; *E. aucklandica*: 63%). Fencing was present alongside 37% of reaches in which *E. menziesii* were present, compared to 48% of sites for *E. aucklandica* (Table 4).

Table 4. Terrestrial habitat characteristics and percentage breakdown at the reach scale for all sites surveyed and sites in which *E. menziesii* and *E. aucklandica* occurred.

Terrestrial habitat characteristics	Total sites	Sites with *E. menziesii*		Sites including *E. aucklandica*	
Dominant vegetation		**n**	**%**	**n**	**%**
Pasture	69	44	69.8	22	81.5
Forestry	19	6	9.5	1	3.7
Retired Grass	8	3	4.8	3	11.1
Native Shrub	20	8	12.7	1	3.7
Parkland	4	2	3.2	0	0
Total	120	63		27	
Canopy cover					
Open	40	16	25.3	8	29.6
Partly shaded	55	38	60.3	17	63.0
Significantly shaded	25	9	12.4	2	7.4
Total	120	63		27	
Fencing					
Complete both sides	32	21	33.3	6	22.2
One side/partial both sides	30	19	30.1	8	29.7
None/ineffective	58	23	36.5	13	48.1
Total	120	63		27	

Mean wetted channel widths were 3.7 m at sites without mussels compared to 5.8 m at sites which contained both species, with mean wetted widths of 4.8 m at all surveyed sites (Table 5). Mean water depths were 0.5 m at sites without mussels, and 0.7 m at sites containing both mussel species. Sites with mussels present had mean water temperatures (measured in summer/autumn) that were slightly, but not significantly cooler than those without mussels. Dissolved oxygen was slightly (but not significantly) lower at sites with mussels present than those without, while specific conductivity was slightly (but not significantly) higher at sites with mussels present than those without (Table 5).

Table 5. Mean (± standard deviation) sample reach characteristics across all sites, and sites in which *Echyridella menziesii* and/or *E. aucklandica* were present. Physicochemical data are means of point measurements) taken across years 2013-2019 on sample occasions in the months January to May.

	Sites with *E. menziesii* present	Sites including *E. aucklandica* present	Sites with no mussels	All sites
Thalweg water depth (m)*	0.6±0.4	0.7±0.4	0.5±0.4	0.5±0.4
Wetted width (m)*	4.8±3.5	5.8±3.8	3.7±6.3	4.6±4.4
Water temperature	15.5±2.5	15.6±2.3	16.7±2.2	16.1±2.5
Dissolved oxygen (%)	92.3±11.7	94.8±8.8	96.7±20.6	95.6±11.7
Dissolved oxygen (mg/L)	9.3±1.3	9.5±0.9	9.6±1.7	9.5±1.3
Specific conductivity (mS/m)	18.7±14.5	17.7±13.9	16.3±21.7	17.3±17.7

* x̄ ± SD of transects evenly-spaced every 5 m along sampling reach.

Streambeds across all surveyed study reaches in which mussels were present were largely characterised by unconsolidated bottom substrates dominated by finer particles including silt (x̄ = 27.5±21.5%), small gravel (x̄= 19.5.5±17.2%) and sand (x̄= 17.5±2.7%) (Figure 12). Mussels of both species were most prevalent within silt substrates (51% of *E. aucklandica*; 48% of *E. menziesii*), with low proportions of individuals associated with other substrate types (Figure 12, Appendix 4).

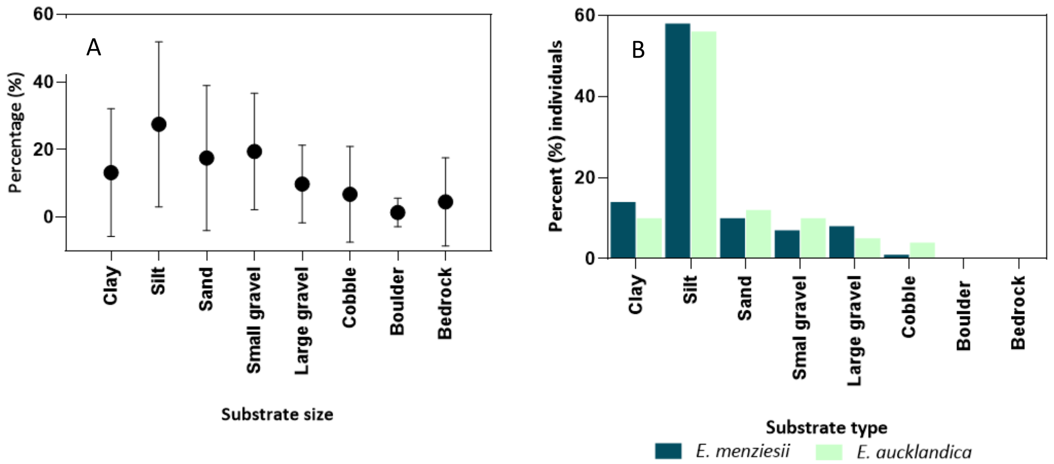


Figure 12. A) Percent (%) substrate composition (mean ± SD) measured across the 50 m survey reaches in which mussels were present (n = 63), and B) percentage of *Echyridella menziesii* (blue, n = 1960) and *E. aucklandica* (green, n = 591) found within each substrate category at sites where mussels were found.

Surveyed sites had a range of substrate embeddedness, perhaps unsurprisingly given the catchment position and gradient of many sites. The largest proportion of sites were classified as being dominated (50-75%) by fine particles irrespective of the presence of mussels (Figure 13a). Moreover, the largest proportion of sites surveyed (sites with *E. menziesii* (72%), *E. aucklandica* (77%), and no mussels (60%)), were classified as having low substrate compaction (I = substrates no packing, easily moved, or II = substrates with mostly a loose assortment with little overlap; Figure 13b), although mussels were recorded across all four compaction categories.

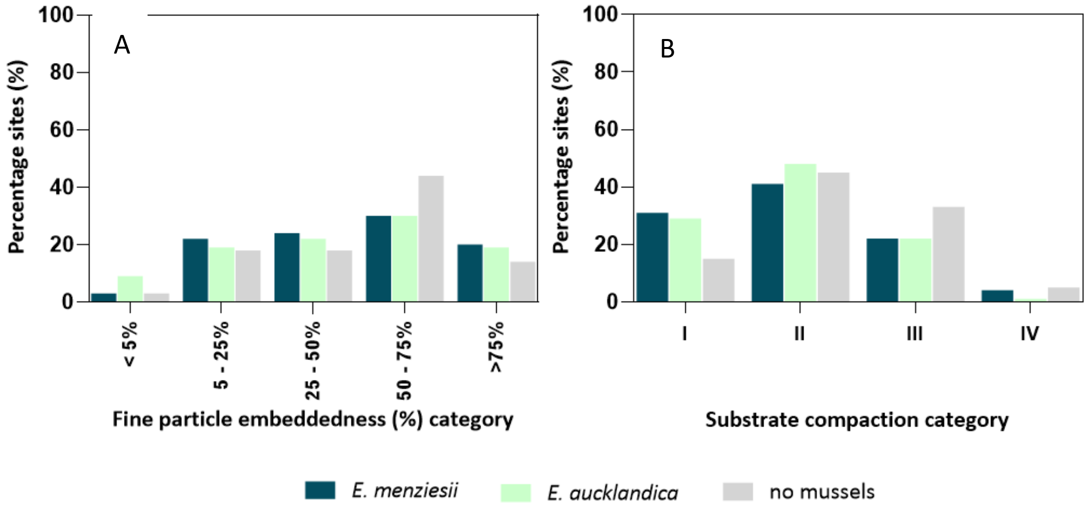


Figure 13. Fine particle embeddedness (A) and substrate compaction (B) category distribution of percentage sites in which *Echyridella menziesii* (n = 63), *E. aucklandica* (n = 27) and no mussels (n = 157) were found. Substrate compaction category: I = No packing, easily moved, II = Mostly a loose assortment with little overlap, III = Moderately packed with some overlap, IV = Assorted sizes, tightly packed and/or overlapping.

Across all sites where mussels were present, runs were the most frequently occupied flow habitat type (75% *E. menziesii* and 80% *E. aucklandica*), followed by pool habitats (17% *E. menziesii* and 23% *E. aucklandica*). Riffles contained the lowest percentages of both species (Table 6). Most measured individuals (83% *E. menziesii*; 81% *E. aucklandica*) were found associated with habitats along the riverbanks, while fewer were found mid-river (17% *E. menziesii*; 19% *E. aucklandica*). Additionally, most individuals of both species (65% *E. menziesii*, 78% *E. aucklandica*) were found on straight sections of stream, followed by outside bends (31% *E. menziesii*, 20% *E. aucklandica*) with few individuals occurring on inside bends (Table 6).

Echyridella menziesii mostly occupied bank toe microhabitats (31%), followed by associations with no apparent surrounding instream habitat feature (26%), undercut banks (16.1%) and woody debris (12%). While *E. aucklandica* was most often associated with no apparent nearby microhabitat (37%), followed by bank toe microhabitats (35%), and woody debris (18%). Microhabitats in which the least proportion of both mussel species were found were sandbanks, and larger substrates, including cobbles and boulders (Table 6).

Table 6. Number of individuals measured and the habitat types (flow, channel side, channel position, microhabitats) they were associated with, for all sites in which both mussel species were found. Highest percentages are in bold.

Habitat association	*E. menziesii*		*E. aucklandica*	
Flow	**n**	**%**	**n**	**%**
Pool	328	17.2	128	22.5
Run	1527	**80.3**	427	**74.9**
Riffle	12	0.6	12	2.1
Backwater	25	1.3	2	0.4
Other	10	0.5	1	0.2
Total	1902*		570	
Channel side				
True Left	759	39.8	242	**42.5**
True Right	831	**43.6**	221	38.8
Middle	317	16.6	107	18.7
Total	1907		570	
Channel position				
Outside bend	594	31.1	114	20.0
Inside bend	75	4.0	13	2.3
Straight	1238	**64.9**	443	**77.7**
Total	1907		570	
Microhabitat				
Bank toe	582	**30.5**	200	**35.0**
Undercut	307	16.1	24	4.2
Wood	225	11.7	104	18.2
Macrophytes	181	9.5	24	4.2
Root mat	83	4.4	7	1.2
Bedrock/Boulder/Cobble	18	1.0	2	0.4
Sand bar	9	0.5	2	0.4
No habitat feature	502	26.3	209	**36.6**
Total	1907		570	

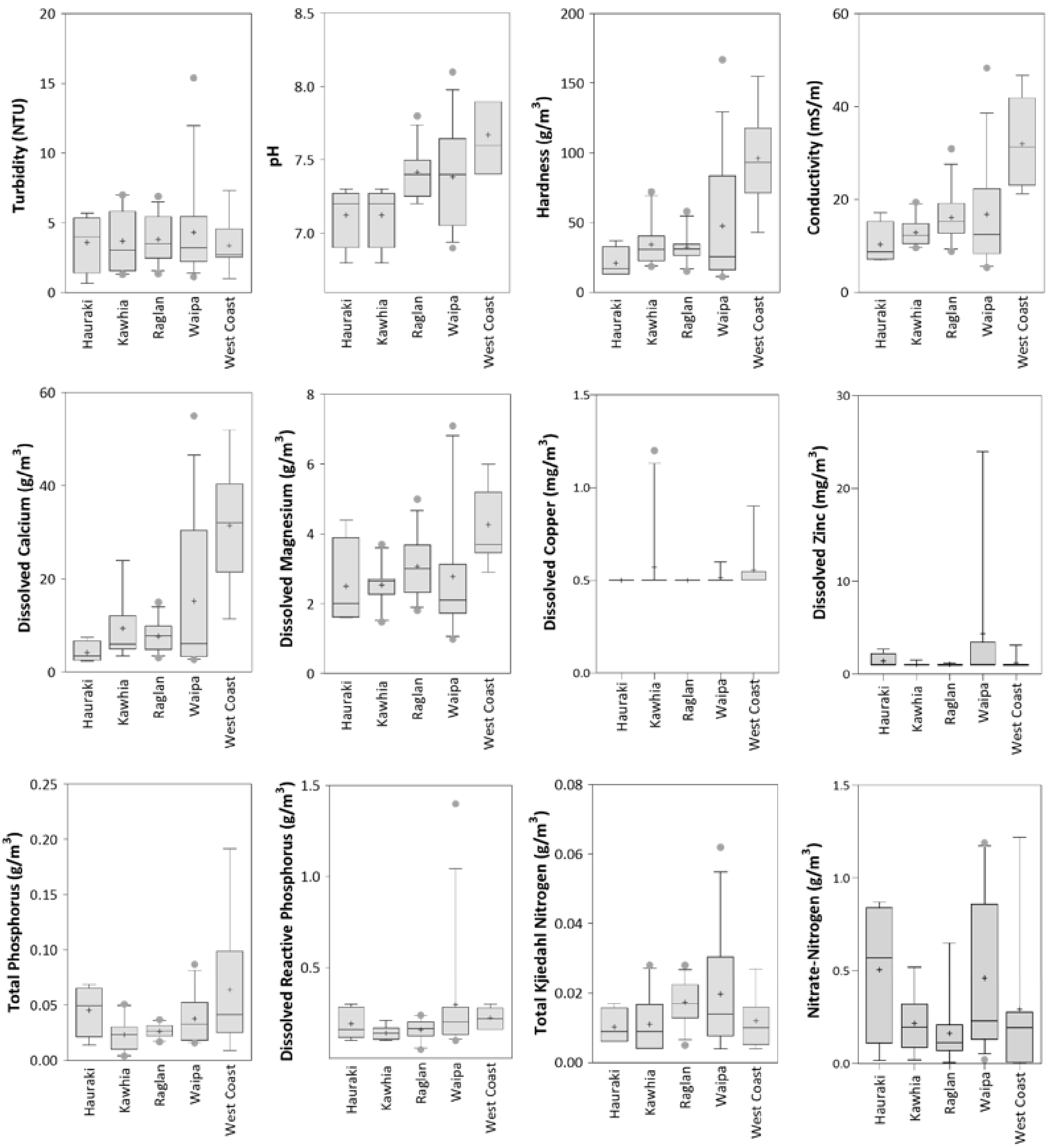
NB*: Lower number of total mussels assessed for *E. menziesii*, as flow types were not recorded for some individuals.

3.4.2 Water quality

Water quality concentrations analysed were relatively low across all catchments, compared to surface waters in New Zealand, with Waipā being the only catchment with relatively larger ranges in nearly all variables tested (except for dissolved copper and total phosphorus). No significant differences were found between sites with and without mussels for any of the water quality parameters tested (all $p > 0.05$; see Table 7) although when sub-catchments were compared for sites with mussels, statistically significant differences were found. pH differed across catchments (K W: 13.9, $p = 0.007$), with significantly lower pH found at Hauraki and Kawhia sites compared to West coast catchments ($p = 0.02$) (Figure 14). Similarly, dissolved calcium concentrations (K-W: 17.8, $p < 0.001$), and electrical conductivity (K-W: 16.7, $p = 0.002$) were significantly higher within the West coast catchment compared to all other sampled catchments (all $p < 0.01$; Figure 14; Appendix 5), while dissolved magnesium concentrations (K-W: 13.5, $p = 0.009$) only differed between the West Coast and Waipā catchments (p = 0.001). The remaining parameters showed no significant differences between catchments (see Figure 14; Appendix 5).

Table 7. Mean ± standard deviation, and Mann Whitney *U* statistics, and *p*-values for each water quality parameter measured across sites with mussels present compared to sites with mussels absent (between the years 2013-2018) Only sites surveyed by Waikato Regional Council are presented in the table.

Water quality parameters	Concentrations at sites with mussels	Concentrations at sites without mussels	*U*	*p*-value
Turbidity (NTU)	3.8±2.4 (0.7-15.4)	5.7±5.3 (1.1-22)	613	0.3
pH	7.4±0.3 (6.8-8.1)	7.4±0.4 (6.8-8.3)	573	0.13
Hardness (g/m^3 $CaCO^3$)	44.2±35.1 (11.1-155.9)	33.9±15.2 (11.8-63.0)	699	0.6
Electric conductivity (mS/m)	16.8±9.2 (5.3-43.0)	13.0±4.1 (5.6-18.7)	556	0.09
Dissolved Calcium (g/m^3)	12.6±12.8 (2.4-55.0)	9.4±5.8 (2.9-21.0)	722	0.8
Dissolved Magnesium (g/m^3)	3.1±1.3 (0.9-7.1)	2.6±1.1 (1.1-6.1)	559	0.07
Dissolved Copper (mg/m^3)	0.5±0.1 (0.5-1.0)	0.5±0.1 (0.5-7.0)	529	0.9
Dissolved Zinc (mg/m^3)	2.0±5.0 (1.0-32)	1±0.1 (1.0-3.0)	432	0.4
Total Phosphorus (g/m^3)	0.03±0.02 (0.004-0.2)	0.03±0.01 (0.004-0.08)	595	0.3
Dissolved Reactive Phosphorus (g/m^3)	0.2±0.2 (0.05-1.4)	0.2±0.1 (0.02-0.64)	647	0.6
Total Kjeldahl Nitrogen (g/m^3)	0.02±0.01 (0.004-0.06)	0.02±0.01 (0.004-0.04)	578	0.2
Nitrate-Nitrogen (g/m^3)	0.3±0.3 (0.002-1.2)	0.2±0.2 (0.04-0.7)	700	0.8
Total Ammoniacal-Nitrogen (g/m^3)	0.02±0.02 (0.01-0.2)	0.01±0.008 (0.01-0.05)	575	0.4



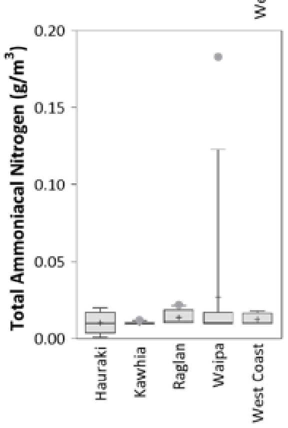


Figure 14. Box plots of water quality parameters for sites containing mussels across all catchments except Lower Waikato. Box boundaries indicate interquartile ranges; within each box are the mean (+) whiskers are 10th and 90th percentile, while outer circles denote outliers.

4 Discussion and recommendations

4.1 Mussel distribution and abundance

This study has increased the documented knowledge of the distribution and abundance of riverine populations of *Echyridella menziesii* and *Echyridella aucklandica* (see Fenwick & Marshall, 2006). Our surveys of Waikato streams showed that *E. menziesii* was more widespread (63 of 120 sites) and abundant than *E. aucklandica* which was found with limited occurrences (27 of the 120 sites). Individuals of *E. menziesii* occurred at all sites in which live mussel species were detected, and were found with and without *E. aucklandica*, while *E. aucklandica* occurred only in association with *E. menziesii*. *Echyridella aucklandica* were most prominent in coastal sites, but small populations were occasionally found in low abundances at inland sites with good connectivity to the ocean (e.g., up to 70 km inland in the Waipā catchment). Mussel densities (no. per m2) and abundances (no. per 50 m reach) varied across sites and catchments but were generally low for both species (*E. menziesii*: $\bar{x}$ = 0.37 per m2; *E. aucklandica*: $\bar{x}$ = 0.05 per m2). West Coast streams supported populations with the highest densities and abundances of both species. Here, *E. aucklandica* had the highest densities and abundances in the Raglan catchment (likely attributable to the Ohautira Stream site which contained high densities of both species), while *E. menziesii* were found to be most dense and abundant in the upper West Coast and Kawhia catchments. Due to limited distribution and density data of instream mussel populations across New Zealand, it is difficult to compare the densities determined for both mussel species across our 50 m survey sites (<1 mussel per m^2) with other stream populations from other regions. The only other known reported densities of *E. menziesii* in streams were in the Cashmere Stream in Canterbury where density estimates were 0.2 per m^2 (Burdon & McMurtrie, 2009), compared to 0.4 to 12.4 per m^2 in a later survey of the same reach (Instream Consulting, 2020). In contrast, numerous studies exist on *E. menziesii* populations in New Zealand lakes, with mean density estimates ranging from <1 per m^2 in Lake Karāpiro, Waikato (Roper & Hickey, 1994) to 160 per m2 in Lake Rotokawau, Bay of Plenty, and 6 per m2 across several North and South Island lakes (Walker et al., 2001 and references therein).

Globally, reported densities of mussel populations range from 0.08-0.4 per m^2 for *Unio crassus* in streams within the Danube catchment (Stoeckl et al., 2014), to 2.3-22.7 per m^2 for *Margaritifera margaritifera* in central Sweden streams (Österling, 2015). Numerous studies relate population density to the number of recent recruits with higher densities of small mussels, and to host fish density (Stoeckl et al., 2014; Österling, 2015). As mussels naturally occur in aggregations that are patchily distributed (Hastie et al., 2000; Strayer et al., 2004), populations can be inherently difficult to quantify, thus the absences or low densities (e.g., *E. menziesii* and *E. aucklandica* absent from approximately 48% and 77% of the surveyed sites, respectively) in our surveys may be partly attributed to the selection of short sampling reaches that may not have captured aggregations. Moreover, deeper pools within some reaches weren't able to be assessed, potentially leading to underestimates of densities, as these habitats can support aggregations of mussels. Notwithstanding potential underestimates due to sampling constraints, one of the main variables associated with mussel distribution and abundance is the host-mussel relationship, notably the historical patterns of host fish distribution and the current availability of host species during the mussel reproductive period (Vaughn and Taylor, 2002; Strayer et al., 2008; Österling, 2015; Modesto et al., 2018). Mussels have complex reproductive cycles in which their larvae (glochidia) are temporary parasites on fish, that depend on the distribution and abundance of their host to survive (Barnhart et al., 2008). Recent studies indicate that *E. menziesii* is a host generalist, relying on a wide range of native fish species for recruitment, including a number of *Gobiomorphus* (bully) (Brown et al., 2017; Hanrahan, 2019). *Echyridella aucklandica*, in contrast, appears to be a host fish specialist, currently known to metamorphose on only one native New Zealand fish species, the common smelt (*Retropinna retropinna*; Melchior et al., 2021; Melchior, 2021). Interactions between mussels and their hosts can easily be disrupted, particularly for species with high host specificity. In New Zealand, a large portion of the potential host fish pool is diadromous (McDowall, 1990), and migration both upstream and downstream may be disrupted or limited by obstructions to fish passage (Ward et al., 1987; McDowall, 1995; Franklin & Gee, 2019), particularly for the *E. aucklandica* host, common smelt, which has poor climbing ability. In contrast, host-generalists like *E. menziesii* likely has greater recruitment and thus dispersal potential due to access to a wide range of available host resources, leading to increased distributions and greater abundances (Vaughn, 2012).

As only scant historical data on the distribution and abundance of both *E. menziesii* and *E. aucklandica* is available, it is not entirely clear, based on density data only, whether the low densities in our surveys reflect an actual decline in both species populations across the general Waikato catchment, or whether low densities are a result of horizontal patchiness and sampling limitations (but see section 4.2 on mussel size structure). Nonetheless, accounts of mussel populations having in the past (approximately 60 years ago) been present in the Waikato mainstem, where they now appear to be absent, suggest that severe declines may have occurred in the Waikato River catchment (pers. Comm S. Clearwater, 2022; Waikato River Integrated Scoping Study, 2010). Proposed density bands for streams and rivers sampled using the protocol of Catlin et al (2018), developed for comparisons of population densities and status over time and across different regions (based on Hastie et al., 2000), indicated that most *E. menziesii* sites sampled in this report were classified as 'C' (Locally Occasional). *Echyridella aucklandica* were 'Locally Absent' (E) throughout most of the region, with those sites in which *E. aucklandica* were present, tending to have a range of classifications; from 'D' (Locally Rare) to some which were classified as 'A' (Locally Common). This approach used both density and abundance data for easier interpretation and to encourage standardised reporting when making comparisons across streams. Although a wide range of sites were sampled across catchments in the middle and western Waikato, more surveys are needed in the eastern region, including the Hauraki, Coromandel, and lower Waikato, to further increase understanding of spatial distribution and abundances of both species, particularly for *E. aucklandica.*

4.2 Population size structure

Because there is no universal definition of the juvenile stage, this report used mussels below the lengths 30 mm in *E. menziesii* and 40 mm in *E. aucklandica* as an index of recruitment. These size thresholds were based on age length estimations for *E. menziesii* (30 mm: 2-4 years) from Grimmond (1968) and James (1985), as used by Rainforth (2008), and estimated length at sexual maturity observed for both *E. menziesii* and *E. aucklandica* by Melchior (2021). Evidence of recent juvenile recruitment was generally lacking for both species, particularly for *E. aucklandica* populations for which size frequency distributions were skewed toward large individuals. *Echyridella menziesii* on the other hand, appeared to show some populations with mussel lengths spread relatively evenly across most size classes (except for below 20 mm). The scarcity of smaller individuals is a common finding in population surveys of mussels (Strayer et al., 2008; Melchior, unpublished data). Low numbers of juveniles may be due to a combination of detection sampling bias towards older adult mussels, direct and indirect biotic and abiotic factors affecting juvenile development and survival (Hastie et al., 2000; Ries et al., 2015; Miura et al., 2021; Goldsmith et al., 2021), or recruitment pulses causing annual variations in juvenile numbers due to temperature changes or hydrological conditions causing mismatches in the timing between host abundance and larval release (James, 1985; Morales et al., 2006, Melchior et al., 2021). Because juvenile mussels are small, inconspicuous, and can occupy microhabitats that are distinct from that of adults, i.e., buried up to 10 cm within benthic substrates (Bauer, 1988; Geist & Auerswald, 2007; M Melchior unpublished data), their numbers can easily be underestimated, especially for newly settled juveniles which have minimum diameters at metamorphosis of ~0.3 mm for *E. menziesii* and ~0.5 mm *E. aucklandica* (Melchior et al., 2021). Thus, juvenile mussels in a population could go undetected for many years using visual and tactile search methods, until mussels are large enough to move up to the surface of the stream bed (Geist & Auerswald, 2007). Nonetheless, the very low numbers of *E. aucklandica* individuals below 70 mm at most sites and sub-catchments in this study is not easily explained by sampling deficiencies of juveniles or by annual variations of recruitment. Because, overall, *E. aucklandica* size-frequency distributions would be expected to have a wider range of lengths across size classes, with less deviation from normality toward older age classes. That is, small to medium-sized individuals (i.e., lengths below 70 mm) would be expected to be in greater abundances than those shown in the current study. In this context, the apparent lack of juveniles in combination with the low densities of *E. aucklandica* found throughout the region is of concern for the conservation management of this 'Threatened – Nationally Vulnerable' species.

More plausible explanations for low recruitment are that unsuitable host fish species or insufficient fish densities are present to host *Echyridella* species (Österling et al., 2008; Stoeckl et al., 2014; Modesto et al., 2018; Melchior et al, 2021; Kawajiri et al., 2021). Mussel and fish densities may be affected by anthropogenic stressors including fish passage obstructions to migratory species and sensitivity to water quality degradation, particularly increases in total suspended sediment which has been associated with declines in fertilisation success, glochidia development, glochidia attachment and encystment to fish (see section 4.1; Modesto et al., 2018; Franklin & Gee, 2019; Kawajiri et al., 2021; Goldsmith et al., 2021). Environmental stressors may also impair recruitment through direct impacts on juveniles which are considered a highly sensitive life stage. Juvenile mussels can be negatively affected by turbidity and fine sediment, and contaminants including ammonia, copper and zinc (Negus, 1996; Strayer et al. 2004; Geist & Auerswald, 2007; Österling et al. 2010; Clearwater et al., 2014; Lopes-Lima et al., 2017). Miura et al., (2021) recently reported that increases in nutrient concentration and fine silts synergistically caused recruitment failure of mussels by reducing the survival rate of early juveniles.

Based on surveyed densities and size-frequency distributions, our report indicates that populations of *E. aucklandica* are 1) potentially remnant and declining at sites within the West Coast, Waipā, and Kawhia catchments; 2) are declining from Raglan and Hauraki catchments, and 3) are absent from parts of the lower Waikato (although this may be partly attributed to the selection of sampling sites that may not have captured patchy mussel distributions). In contrast, though *E. menziesii* population densities were not high, their size-frequency distributions indicate some ongoing recruitment and likely stable populations from at locations within most sub-catchments. The absence of *E. menziesii* populations from tributaries off the Waikato River mainstem, may again, be attributable to lack of sample sites in the area due to limited clarity, and the length of sampling reaches (50 m), since we know that current and historical populations do exist and have been reported in the area (e.g., lower Waikato River, Lake Karāpiro; pers. Comm S. Clearwater, 2022; Waikato River Integrated Scoping Study, 2010).

To enhance populations of both mussel species, we recommend that riparian restoration and protection is undertaken of surrounding habitat and upstream (tributaries) of current mussel populations. Furthermore, as host fish play an important role in the recruitment of New Zealand mussel species, we recommend ensuring or remediating access (where appropriate) for native fish species with limited climbing abilities that are expected to play a key role in mussel recruitment (particularly common smelt for *E. aucklandica*, Melchior et al., 2021; and bully species for *E. menziesii*; Melchior et al., 2022; Hanrahan, 2019). It is worth ensuring that greater consideration is given to protecting common smelt spawning habitats as they are currently the only known host for *E. aucklandica*. Due to the declining abundances of *E. aucklandica* and, the importance of common smelt for this mussel species (Melchior et al., 2021), conventional surveys paired with eDNA sampling (Ferris, 2020) could be used to determine the accessibility of common smelt to locations where recruitment is/isn't occurring during the *E. aucklandica* glochidia release season (October to March; Melchior, 2021). Furthermore, we recommend targeted surveys of stream reaches and meso-habitats that are expected to be preferred by both mussel species at their adult and juvenile stages. Additionally, we suggest undertaking urgent repeated outcome monitoring surveys at selected locations, that include examination of mussel densities and length-frequency distributions to provide insights into the changing nature of mussel populations of both species within Waikato streams. Last, estimating mussel ages may be a cost-effective research opportunity that could be investigated due to knowledge gaps existing around the ages of *E. aucklandica* in general, and stream populations of *E. menziesii*, which might vary from the ages determined from lake populations by Grimmond (1968), James (1985) and Roper and Hickey (1994).

4.3 Mussel shell shape and condition

Shell morphometry or shape (length:height) varied significantly between species with *E. menziesii* having rounder shells that were higher and shorter than those of *E. aucklandica.* During mussel surveys, the identification of *Echyridella* species is primarily based on their appearance and morphology. Because of the observed morphometrical plasticity of shells within and between species, this can at times lead to misidentifications at sites in which the two species coexist. Length:height ratios could be used as a simple tool to check for misidentification of species through detection of shell shape outliers in the data. In the current report, length: height outliers for *E. menziesii* above 2.5 may be considered as misidentifications of species, as no obvious data input errors were detected during the initial data checking phase of the analysis. Variation in shell shape within species can be explained on the basis of genetic factors and/or environmental influences such as water chemistry, hydrology and temperature (Hastie et al., 2001), and the interaction between them (Falconer & MacKay, 1996; Walker et al., 2001; Zajac et al., 2018). Shell condition measurements in mussels have been recommended for environmental monitoring because they can provide a good indicator of biological and physiological stress (Widdows, 1985). For example, studies have reported that erosion scores are related to physical abrasion through turbulence within streams (Roper & Hickey, 1994; Griffiths & Cyr, 2006; Rainforth, 2008). Our report found that most individuals of both species showed minimal outer erosion, likely due to a high proportion of sites being lowland, low gradient streams where waterborne abrasion would be limited. Roper and Hickey (1994) partly related erosion levels of *E. menziesii* to age, with older mussels showing greater abrasion, however this was not found in another investigation of *E. menziesii* in the Whanganui River catchment (Rainforth, 2008). We recommend that, if greater erosion is found present on shells within surveyed sites, further analyses should be undertaken to determine causes. This is important due to mussels with eroded shells having been reported to expend more energy on shell replacement, and less into reproduction, leading to reduced gonad development, which could lead to population declines (Kaehler & McQuaid, 1999).

4.4 Habitat associations

Numerous studies have suggested that increased levels of agricultural activity in catchments may have significant impacts on mussel abundance and richness (Arbuckle & Downing, 2002; Poole & Downing, 2004; Newton et al., 2008; Atkinson et al., 2014; Cao et al., 2015). Impacts have been attributed to increased nutrient, pesticide, herbicide, metal and sediment loading in aquatic systems, which often occur as a result of changing land-use to pasture (Helton et al., 2011 Woodward et al., 2012; Clearwater et al., 2014; Garcia et al., 2017). In our study, water quality concentrations analysed were relatively low across all catchments (except for Waipā which had relatively larger ranges for almost all variables tested) compared to surface waters in New Zealand. For example, mean ammonia concentrations of 0.02 g/m3 at sites with mussels present, were much lower compared to current ANZECC water quality guideline (95th percentile) trigger values for ammonia exposure of 0.9 mg/L (pH 8) (ANZECC & ARMCANZ, 200; Clearwater et al., 2014). Although debates remain around the role played by sediment, excessive sedimentation due to poor land use practises, is suspected to be one of the major factors of mussel declines since the late 1800s (Kunz, 1898; Goldsmith et al., 2021). Streambeds of surveyed sites in which mussels were found were largely characterised by unconsolidated finer particles (silt, followed by clay, and sand), with both *Echyridella* species most frequently found within silt substrates. Moreover, a large proportion of reaches comprised highly embedded and unconsolidated substrates, indicating that both mussel species live in depositional habitats prone to sedimentation.

Suspended solids have been reported to impact mussels by decreasing food availability, physically interfering with filter feeding and respiration, and impeding various aspects of the mussel-host relationship (including reproduction and glochidia metamorphosis; Rainforth, 2008; Vaughn & Hakenkamp, 2001; Gascho Landis et al., 2013; Goldsmith et al., 2021). Increases in fine particles within streams have been reported to impact juveniles due to their sensitivity to smothering, with mortality occurring at sedimentation depths as low as 0.6-2.5 cm (Goldsmith et al., 2021). Moreover, numerous studies have shown that high ammonia levels, which can occur in organic-rich deoxygenated sediments, are toxic to juvenile mussels and glochidia (Augspurger et al., 2003; Newton & Bartsch, 2007; Wang et al., 2008; Strayer & Malcom, 2013; Bril et al., 2017).

Because juveniles have different habitat requirements to adults, living buried up to 10 cm stream bed depths for the most part of their early life stage (Geist & Auerswald, 2007), juveniles may be more impacted by land-use change than adults. Fine sediment runoff in the Waikato region may therefore be a potential factor limiting successful recruitment of mussels and needs further investigation. The surveyed *Echyridella* species did not show obvious habitat partitioning, with both species most prevalent in relatively shaded run habitats, along stream bank edges, and associated with bank toe micro-habitats (i.e., areas where the streambed meets the riverbank). Micro-habitat types such as these allow individuals to inhabit areas with increased substrate stability and potential flow and predation refugia, as well as increasing the potential for host fish overlap (Hastie et al., 2000; Morales et al., 2006; Armstrong et al., 2003; Haag, 2012; Melchior, 2021). This report showed no significant differences in water quality parameters measured between sites in which mussels were present, and sites in which they were absent. This aligns with the findings by Death et al. (2018) in which no associations with water quality parameters were found when using boosted regression trees to model mussel abundance. We did find differences in physicochemical parameters between catchments, although it should be noted that we collected one-off water samples rather than undertaking in-depth characterisation of the physicochemical properties of each waterway over time.

Inadequate knowledge of mussel habitat requirements and the factors that determine or constrain mussel distribution, may hinder their conservation (Strayer, 2008). More research is required to determine habitat variables that best explain distribution and abundance patterns of *E. menziesii* and *E. aucklandica* over time and across a range of landscape settings. Future studies should include the interaction of biotic, chemical and anthropogenic influences operating on multiple spatial scales (Newton et al., 2008), and investigate micro-habitat and physicochemical factors that affect mussel recruitment (e.g., juvenile habitat).

4.5 Future recommendations

This work explores data on region-wide quantitative mussel surveys from 2013 to 2019 and expands information on the spatial distribution and abundances, population structure and habitat associations of *Echyridella menziesii* and *E. aucklandica* in wadeable Waikato region streams. Importantly, the results presented in this report suggest that most *E. aucklandica* populations occur at low densities and have little to no evidence of recruitment, indicating potentially non-functional, or remnant populations, which could go extinct in the future if no action is taken. Based on data from the baseline surveys across wadeable streams in the Waikato region, we recommend that appropriate planning and species recovery tools are developed and actioned, particularly for *E. aucklandica.* We provide below a number of actionable recommendations, research opportunities and identify council's obligations with regard to threatened species by the National Policy Statement for Freshwater Management (2020).

Actionable restoration activities in lowland environments should include objectives and actions with a focus on freshwater mussels (especially *E. aucklandica*). These should include:

1. Maintaining or remediating access (where appropriate) for native fish species with limited climbing abilities that are expected to play a key role in mussel recruitment (e.g., common smelt for *E. aucklandica*, Melchior et al., 2021; bully species for *E. menziesii*; Hanrahan, 2019);
2. Riparian restoration and protection of habitat around, and upstream (tributaries) of current mussel populations;
3. Outcome monitoring to determine whether populations are continuing to decline or respond positively to management actions;
4. eDNA surveys paired with conventional surveys, to detect common smelt during the *E. aucklandica* glochidia release season, to determine the accessibility of common smelt to locations where juvenile recruitment is/isn't occurring;
5. Targeted surveys of stream reaches and meso-habitats that are expected to be preferred by both mussel species.

We also identify several research opportunities that will enhance *Echyridella* conservation into the future. These include,

1. Investigating the relative effects of biotic (host fish density and distribution; particularly bully species for *E. menziesii* and common smelt for *E. aucklandica*) and abiotic (e.g., fine sediment, water temperature, hydrology and water quality) factors on the recruitment of *Echyridella* species.
2. Identifying key variables and drivers related to distribution, abundance, and persistence of juvenile and adult *Echyridella* populations across temporal (e.g., decadal) and spatial (e.g., catchment) scales. From this, appropriate management mechanisms can be identified, tested, and assessed. Detailed density and shell size information can then be used to assist with producing population indices which reflect the health of a given population.
3. Further research to better understand the biology of mussels including growth and age patterns of lotic *E. aucklandica* and *E. menziesii* populations.

This report contributes key information to enable Waikato Regional Council to perform its duties with regard to threatened species as required by the National Policy Statement for Freshwater Management (2020). Threatened species (i.e., *E. aucklandica*) are a compulsory value in the NPS FM (2020) and their habitats must be identified and any specialised habitat or conditions for them to fulfil their life cycle must be managed to support their existence and recovery. Both species of mussels in the Waikato Region are considered Mahinga kai, which is also a compulsory NPS FM (2020) value. In collaboration with communities, Council will therefore need to develop objectives, polices, and action plans, and we suggest that these should include the following:

1. Remediation of any fish passage barriers that may be impacting access to host fish;
2. Habitat enhancement for both mussels and host fish, particular consideration needs to be given to upstream riparian planting, and critical source zones for sediment, to assist with maintaining water temperature, quality, and reducing sedimentation; factors which may be affecting juvenile survivorship;
3. Ongoing adaptive management surveys examining the outcome of the restoration work;
4. Identification of key catchments for which restoration of populations can be achieved through targeted management and monitoring (could include waterways for which mussels are presently absent, but where this could be resolved);
5. Identification of focal sites for monitoring that provide a mix of low- and high-density populations and can be used to track response to environmental patterns or events (monitoring should include mussel and fish population health, water quality and habitat parameters);

6. Ongoing region- and nation-wide or Freshwater Management Unit scale surveys, utilising reproducible protocols (e.g., McEwan, 2015; Catlin et al., 2018) to ensure persistence of populations across a range of freshwater environs (e.g., lakes, rivers and streams).

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6 Appendices

Appendix 1: Length frequency distribution analyses

Catchment	KS (D)	P value
Hauraki	0.47	<0.0001
Kawhia	0.81	<0.0001
Raglan	0.89	<0.0001
Waipā	0.41	0.0003
West Coast	0.91	<0.0001

Appendix 2. Mean length (mm) and shape (length:height ratio, L:H) in *Echyridella menziesii* and *E. aucklandica* across the six sub-catchments (Lower Waikato only includes length data of *E. menziesii*.)

Catchment	Length (mm)		Length:height ratio (mm)	
	E. aucklandica	*E. menziesii*	*E. aucklandica*	*E. menziesii*
Hauraki	72.3±14.1 (72-88)	61.1±7.9 (25-84)	2.1 (1.9-2.5)	1.7 (1.3-2.2)
Kawhia	87.4±6.8 (71-100)	65.5±11 (20-92)	2.1 (1.8-2.4)	1.8 (1.3-2.3)
Raglan	88.7±11 (36-112)	65.6±7.3 (20-93)	2.2 (1.4-2.6)	1.8 (1.4-2.6)
Waipā	72.3±10.3 (53-97)	61.2±10.1 (19-95)	2.0 (1.8-2.3)	1.7 (1.1-2.6)
West Coast	80.8±4.2 (72-88.5)	56.6±9.9 (25-84)	2.1 (1.7-2.5)	1.7 (1.3-2.2)
Lower Waikato	-	44.3±8.2 (24-67)	-	-

Appendix 3: Number and percentage (%) of mussels assessed to be in each erosion class modified from Roper & Hickey (1994) and Rainforth (2008).

WRC Erosion Category	*Echyridella menziesii*		*Echyridella aucklandica*	
	n	***%***	***n***	***%***
0% no wear on shell surface, slight on beak	22	1	4	1
1-25% surface worn, light wear	1438	78	438	80
25-50% surface worn, light to some wear	272	15	79	14
50-75% surface worn, some deep pitting	64	4	9	2
75-100% surface worn, badly eroded	38	2	14	3
Total assessed	1834		555	

Appendix 4: Number and percentage (%) of individuals measured and the habitat type they were associated with, for all sites in which mussels were found.

Habitat association	*E. menziesii*		*E. aucklandica*	
Substrate	n	%	n	%
Clay	278	14.1	61	10.3
Silt	1142	58.3	333	56.3
Sand	211	10.7	72	12.2
Small gravel	140	7.2	63	10.7
Large gravel	158	8.1	34	5.8
Cobble	23	1.2	24	4
Boulder	4	0.2	4	0.7
Bedrock	4	0.2	0	0

Appendix 5. Kruskall-Wallis test statistics of water quality comparisons between catchments.

Parameter	K-W	*p* - value	Multiple comparisons	*p* - value
Turbidity	0.4	0.978	ns	
pH	13.9	0.007	Hauraki vs. West Coast	0.02
			Kawhia vs. West Coast	0.02
Hardness	18.1	0.001	Hauraki vs. West Coast	0.004
			Kawhia vs. West Coast	0.02
			Raglan vs. West Coast	0.02
			Waipā vs. West Coast	0.006
Electrical Conductivity	16.8	0.002	Hauraki vs. West Coast	0.004
			Kawhia vs. West Coast	0.007
			Raglan vs. West Coast	0.07
			Waipā vs. West Coast	0.02
Dissolved Calcium	17.8	0.001	Hauraki vs. West Coast	0.002
			Kawhia vs. West Coast	0.05
			Raglan vs. West Coast	0.01
			Waipā vs. West Coast	0.03
Dissolved Copper	1.6	0.8	ns	
Dissolved Magnesium	13.5	0.009	Waipā vs. West Coast	0.01
Dissolved Zinc	3.6	0.5	ns	
Total Ammoniacal_N	6.3	0.2	ns	
Nitrate-N + Nitrite-N	5.6	0.2	ns	
Dissolved Reactive Phosphorus	7.9	0.09	ns	
Total Kjeldahl Nitrogen	5.9	0.2	ns	
Total Phosphorus	6.1	0.2	ns	