Determining restoration potential by transplanting mussels of different size classes over a range of aerial exposures

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ABSTRACT: Restoration of mussels typically focuses on either subtidal or intertidal habitats, although it is important to consider the full historical range of a species. However, it remains unclear how environmental changes can impact the ability of mussels to survive in tidal heights where they occurred historically. Additionally, there is limited research on the viability of reducing mussel stock size for restoration purposes. In this study, green-lipped mussels *Perna canaliculus* of 2 size classes (80 and 60 mm) were assessed when transplanted as a single size class or as mixed cohorts in 9 m² plots at 3 shore heights (i.e. neap low tide, spring low tide, and subtidal). The mussels were sampled over a 1 yr period to understand the effect that shore height and size class had on mussel metrics, such as survival, growth, and condition. The results revealed that shore height had a greater effect than size class on mussel survival, with a total loss of mussels transplanted into areas that were exposed at neap tides in contrast to 39% mussel survival transplanted into areas that were only exposed on spring low tides. Further, mussels transplanted in the adjacent subtidal had higher overall survival (74%). This suggests that aerial exposure time determines the upper vertical limit for restoration by transplantation of mussels sourced from aquaculture, despite their historical distribution. The results of this study also support the use of smaller mussels (~60 mm) for transplantation for mussel reef restoration, as a 25% reduction in size resulted in 50% more mussels being deployed.

KEY WORDS: Green-lipped mussels · *Perna canaliculus* · New Zealand · Bivalve · Shellfish · Stock selection · Intertidal

1. INTRODUCTION

Mussels are important reef-building organisms in many coastal ecosystems around the world. They frequently play major ecological roles in coastal environments across both intertidal and subtidal zones (Jeffs et al. 1999, Menge et al. 2007, Petes et al. 2007, Commito et al. 2008), including boosting biodiversity by providing unique habitats especially for juvenile fish and epibenthic organisms (Benjamin et al. 2022a, Sea et al. 2022). Mussel reefs also provide a variety of other ecosystem services, including water filtration (Hawkins et al. 1999, Newell 2004) and denitrification (Hillman et al. 2021, Sea et al. 2021). Like other habitat-forming shellfish species, coastal mussel populations have declined dramatically in many parts of the world, including a loss of 53% of mussels in Europe, North America, and Australia (Lotze et al. 2006).

Growing recognition of the global loss of reef-building coastal shellfish populations has led to widespread calls for greater efforts toward their restoration (Beck et al. 2009, 2011, Bayraktarov et al. 2016, Fitzsimons et al. 2019). However, shellfish res-

toration has been largely focused on oysters, while, by comparison, mussel restoration research and practice are in their infancy (Bayraktarov et al. 2020, Toone et al. 2021). Transplantation of living mussels for restoring mussel reefs is costly and can be hindered by many different issues, including predation (Wilcox & Jeffs 2019, Alder et al. 2021b), lack of sufficient substrate for attachment causing dislodgement (Capelle et al. 2019, Temmink et al. 2021), burial with sediment (Wilcox et al. 2018, Temmink et al. 2021), and hydrodynamic conditions (de Paoli et al. 2015). Furthermore, the issues facing successful transplantation of mussels are not uniform and instead can vary due to many factors, including differences in environmental or ecological conditions associated with location (e.g. Benjamin et al. 2023).

Locations where mussel reefs occurred historically are often targeted for restoration (Fitzsimons et al. 2019, 2020). However, environmental changes, including increasing temperatures and extreme temperature events caused by climate change, can result in mussels being unable to survive in locations and tidal heights where they used to exist, due to oxidative stress and desiccation (Petes et al. 2008b, Sorte et al. 2017, Andrade et al. 2019). Also, the transplantation of mussels for restoration typically focuses on one shore height alone (i.e. just intertidal or just subtidal; e.g. Wilcox et al. 2018, Schotanus et al. 2020a, Temmink et al. 2021), which has the potential to result in incomplete restoration to historically important natural ranges of the target organisms. Further, the transplantation of mussels sourced from aquaculture may pose limitations, as cultured mussels are acclimated to a narrow range of environmental conditions as compared with historical habitats with more challenging environmental regimes. For example, attempts to restore mussel reefs into the intertidal zone by transplanting subtidally cultured mussels have failed due to differences in environmental stress including exposure to variable air temperatures (e.g. Lesser 2006, Lesser et al. 2010, de Paoli et al. 2015). However, transplanting mussels in the subtidal zone can expose them to higher abundances of predators, such as sea stars, which are intolerant to aerial exposure in the intertidal (Petes et al. 2008a). There is a need to develop and test effective methods for restoring mussel reefs to a full range of locations and shore heights in regions where they were historically abundant (Capelle et al. 2019, Alder et al. 2021b, Temmink et al. 2021).

Using smaller cultured mussels for transplantation in restoration, as opposed to fully grown larger mussels, has the potential to improve restoration outcomes, as smaller individuals may be more adaptable in stressful locations, including the intertidal zone. For example, smaller mussels have been shown to have higher phenotypic plasticity (Schotanus et al. 2019) and stronger byssus attachment (Hickman 1979, Alder et al. 2021b). Additionally, the use of smaller mussels provides more mussels per unit of weight for transplantation, which can increase the final density and/or spatial scale and reduce the costs of translocating individual mussels into locations for restoration. Transplanting and installing higher mussel densities have been shown to provide benefits for mussel reef restoration, including increased protection from predation and increased anchorage of mussels with conspecifics to help prevent dislodgement (Commito et al. 2008, de Paoli et al. 2017, Bertolini et al. 2018, Schotanus et al. 2020b). There may also be advantages of mixing sizes of mussels together for restoration, as mixed sizes of mussels may be more representative of natural populations, with adult mussels providing protection for smaller mussels (Frandsen & Dolmer 2002). Few studies have examined the use of smaller mussels for restoration (e.g. Schotanus et al. 2020a, Alder et al. 2021a), while the potential benefits of using mussels of mixed sizes, particularly in the intertidal zone where smaller mussels may have an advantage, remain largely unexplored.

This study aimed to test 2 factors: (1) the effect of aerial exposure on transplantation success of mussels sourced from aquaculture and (2) the relative performance of mussels of 2 different size classes (i.e. ~60 versus 80 mm shell length) when transplanted to different aerial exposures, either in their own size classes or in mixed cohorts.

2. MATERIALS AND METHODS

2.1. Study area and location description

The endemic green-lipped mussel *Perna canaliculus* was historically abundant in both the intertidal and subtidal zones on many parts of the coast around New Zealand (Jeffs et al. 1999). Overharvesting in the last century has resulted in the loss of extensive areas of natural mussel reefs, although the species is now the basis of large-scale aquaculture production (e.g. Paul 2012, Toone et al. 2022). Initiatives aimed at restoring natural subtidal mussel reefs using mussels sourced from aquaculture are underway in at least 3 parts of the country (i.e. Hauraki Gulf, Wilcox et al. 2018, Alder et al. 2021b; Marlborough Sounds, Benjamin et al. 2023; Ōhiwa Harbour, Paul-Burke et
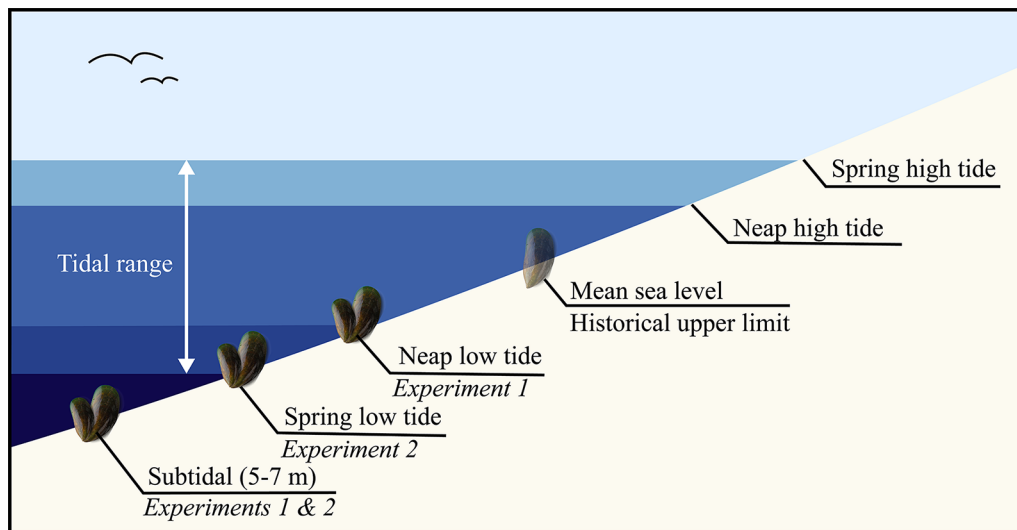
Fig. 1. Two experimental intertidal shore heights used in this study. Expt 1 tested mussels exposed at neap low tides, and Expt 2 tested mussels exposed at spring low tides only. The historical upper limit for green-lipped mussels was mean sea level for the study area, Kenepuru Sound (Flaws 1975)

al. 2022), but restoration of this mussel species to intertidal habitats has been limited (i.e. Toone et al. 2023b). Scattered patches of remnant green-lipped mussels have been recorded in the low-intertidal in parts of the Marlborough Sounds (Toone et al. 2023a); however, historically, mussels were extensive throughout a greater part of the intertidal zone (Flaws 1975). It is currently unknown at what tidal height green-lipped mussels can survive when transplanted from subtidal aquaculture to form mussel reefs and whether different size classes of mussels provide any benefits.

The study area, Kenepuru Sound, is located in the inner Pelorus Sound/Te Hoiere in the Marlborough Sounds, New Zealand, and until the early 1970s had extensive reefs comprised of green-lipped mussels until they were removed by intensive commercial fishing activity in the subtidal (dredging) and intertidal (hand-picking) (Stead 1969, Flaws 1975, Toone et al. 2023a). Historically, the upper tidal limit for wild green-lipped mussels in Pelorus Sound was at mean neap high tide and, specifically in Kenepuru Sound, was located around mean sea level (Flaws 1975; Fig. 1). The 2 locations in Kenepuru Sound chosen for each experiment were Double Bay (Expt 1) and Skiddaw (Expt 2). These locations were selected as they historically supported extensive intertidal mussel reefs, have scattered living individual mussels in the low-intertidal zone (Toone et al. 2023a), and are similar sheltered bays 3.5 km apart with little wave action and relatively large tidal ranges (mean spring tidal range 2.6 m). Both locations have a gently

sloping intertidal zone that is covered with a mixture of cobbles (64–256 mm diameter) and pebbles (2–64 mm) on the Wentworth scale (Wentworth 1922) and a subtidal zone with muddy sediment with no existing emergent habitat.

2.2. Mussel deployment

In June 2021, 10 t of large mussels (mean ± SE shell length = 81.0 ± 1.0 mm, n = 120) and 10 t of smaller mussels (mean shell length: 61.6 ± 0.9 mm, n = 109) were each harvested from Pelorus Sound/Te Hoiere and deposited on the seabed into 2 experiments on the same day. These 2 mussel sizes (~60 and 80 mm) were chosen for this study as this was available donated stock from the aquaculture industry at the time of deployment. Each experiment included a total of 18 plots of mussels over 2 tidal heights, i.e. 9 plots in the intertidal (exposed at low tide) and 9 plots in the subtidal (5–7 m depth; Fig. 2). The deployment was performed at high tide, and at each plot, a 500 kg bag of mussels was lowered into the water from a mussel-harvesting barge and upended to empty it. For both experiments and within each depth there were 3 different plot designs comprising 3 replicates: (1) all large mussels (~80 mm), (2) all small mussels (~60 mm), or (3) a mix of equal weights (250 kg each) of large and small mussels (Fig. 2). The mussels in each plot in the intertidal were spread out after deployment to cover an area of approximately 9 m^2 to match the extent of the subtidal plots, be-
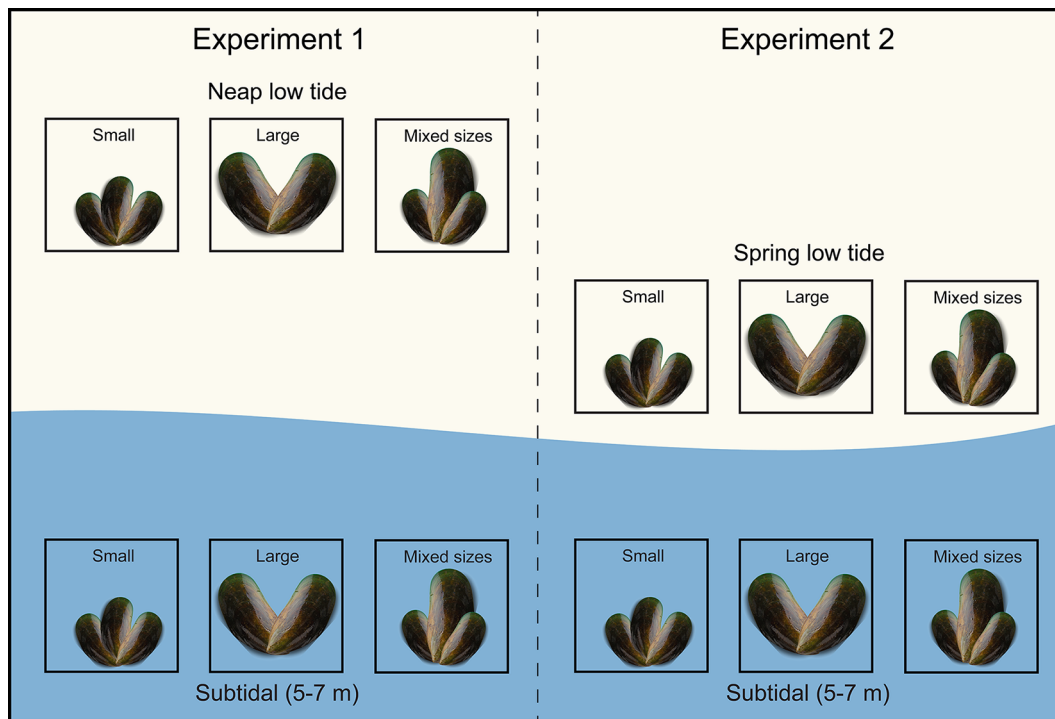
Fig. 2. Study design with 2 experiments. Expt 1 tested mussels exposed at neap low tides, and subtidal shore heights, and Expt 2 tested mussels exposed at spring low tides only, and subtidal shore heights. At each shore height, the 3 size classes (i.e. large mussels, small mussels, and mixed cohorts) each had 3 replicate plots

cause upending the bags in these shallow depths created smaller plots at deployment. In Expt 1 at Double Bay, mussels were placed into the mid-intertidal zone, where they were exposed at neap low tides, and in the subtidal zone (5–7 m; Fig. 1). In Expt 2 at Skiddaw, mussels were placed in the intertidal zone, where they were only exposed at spring low tides, and in the subtidal zone (5–7 m; Fig. 1).

2.3. Sampling design

Both experiments were sampled at the same time intervals and using the same methods. All 18 plots were sampled at deployment (June 2021) and again at approximately 1, 4, 6, and 12 mo after deployment (i.e. August 2021, October 2021, January 2022, June 2022). Mussel survival and deployment density were measured by randomly placing a 0.25 × 0.25 m quadrat 3 times in each plot, avoiding 0.5 m from the edge of the plot and recording the number of dead and live mussels inside each quadrat (Benjamin et al. 2022a,b). All mussels were removed from the quadrat and counted, taking special care to look for new mussel recruits (<30 mm), and then the mussels were returned to the mussel plot. Mussel survival for

each restored plot was calculated as the proportion of live mussels out of the total of both live and dead mussels recorded for each quadrat. The subtidal plots in each location were sampled by divers working on SCUBA, and the intertidal plots were monitored at spring low tides when the mussels were exposed.

Mussel condition and shell length were determined from 10 haphazardly collected mussels from each restored plot at deployment (June 2021) and at the 12 mo sampling (June 2022). For condition, mussels were stored at −20°C, then shucked and the flesh and shells dried at 60°C for 48 h and weighed. The dry condition index was determined using the following formula: dry weight of flesh × 100 / dry weight of shell (Lucas & Beninger 1985). At the 12 mo sampling event, the mussels exposed at neap low tides in Expt 1 had 0% survival and could therefore not be sampled for length or condition.

The abundance of a common New Zealand mussel predator, the eleven-armed sea star *Coscinasterias muricata*, was determined in the plots at each sampling event by placing a transect line running across the centre of each plot and counting all sea stars located 1 m on either side of the transect.

One subtidal plot of large mussels in Expt 2 was not sampled at deployment, due to logistical issues, but

was sampled in all subsequent sampling events. Additionally, 1 intertidal plot of large mussels in Expt 1 was completely lost at the 4 mo sampling event, as it appeared to have been widely dispersed during a storm event and could not be resampled.

2.4. Temperature recording

To record the temperatures and exposure time that the intertidal mussel plots were experiencing in austral spring and summer, 1 HOBO temperature logger (Onset Computer) was deployed amongst the mussels in the middle of each of the 18 plots in the intertidal zone, i.e. 9 loggers in the intertidal zones in each experiment. The loggers were deployed on 18 November 2021 and recorded hourly temperature (water or air depending on tidal cycle) until the final sampling on 17 January 2022. To quantify exposure time at each intertidal plot, temperature data from a full 29 d tidal cycle were analysed, and any hourly data point that was 1 SD colder or hotter than the mean temperature was quantified as exposed. Exposures during low tides determined from the temperature loggers were verified against tidal chart data. Temperature metrics were determined for each experiment (i.e. mean, median, range), as well as the time exposed to extreme temperatures (>40°C).

2.5. Statistical analyses

The data from the 2 experiments were analysed separately. Firstly, assumptions of normality and equivalence of variance in all the data were assessed visually using quartile–quartile plots, which tested the residuals for normality, and then Shapiro-Wilk tests were performed. To identify differences in the performance of mussels between shore heights and among mussel sizes for each experiment separately, all measured metrics (i.e. mussel survival, condition, and sea star counts) were assessed using linear mixed-effect models (LMEs) with shore height, size class, and time as fixed factors and plot number assigned as the repeated measure to account for the repeated sampling performed on the same plots over time. All LMEs were performed in the R package 'lme4' (Bates et al. 2015), and the R package 'cars' was used to determine F-statistics and p-values from the models (Fox & Weisberg 2019). Post hoc comparisons were used to understand significant differences with the R package 'emmeans' (Lenth 2018). To determine temperature differences between the inter-

tidal shore heights, a pairwise Wilcoxon test was used, as the temperature data did not meet the assumptions of normality for a parametric test. All tests were performed using R statistical software version 3.2.3 (R Core Team 2021), and results were considered significant at p < 0.05.

3. RESULTS

3.1. Deployment density, survival, and recruitment

At deployment, the plots with small mussels (60 mm) had a mean of 1.5 times more mussels m^{-2} then the plots with large mussels (80 mm) across both experiments (mean ± SE mussels m^{-2}; small: 2682 ± 251; large: 1818 ± 135; mixed: 2113 ± 210). This indicated that a mussel size reduction of 25% resulted in 50% more mussels deployed using the same weight (500 kg).

Mussel survival did not differ between the 2 mussel size classes or the mixed cohorts in either experiment (LME, Expt 1, $F_{2,77} = 0.366$, p > 0.05; Expt 2, $F_{2,79} = 0.318$, p > 0.05). However, mussel survival did differ by shore height for both experiments regardless of size class (i.e. large, small, and mixed cohorts of mussels; LME, Expt 1, $F_{1,4} = 26.44$, p = 0.007; Expt 2, $F_{1,4} = 114.35$, p = 0.02). Mussel survival was higher in the subtidal plots than in the intertidal plots for both experiments (Table 1). The intertidal mussels in both experiments had similar survival until the 4 mo sampling period, which thereafter resulted in large losses of mussels, particularly for the mussels exposed at neap low tides in Expt 1, which lost 61.2% of mussels between the 4 and 6 mo sampling point, leaving only 18.4 ± 3.0% mussels remaining (Fig. 3). By 12 mo, the mussels exposed at neap low tides in Expt 1 had 0% mussel survival, while there was 38.9 ± 4.9% mussel survival in the plots exposed only at spring low tides in Expt 2 (Fig. 3, Table 1). The subtidal plots for both experiments had similar mussel survival after 12 mo, i.e. Expt 1, 73.9 ± 3.1% and Expt 2, 74.8 ± 2.5% (Fig. 3, Table 1). No juvenile recruitment was visually detected in either of the experiments over the course of the 12 mo.

3.2. Mussel length and condition

At deployment, the 3 types of mussel plots (i.e. large, small, and mixed) all significantly differed from each other in shell length for both experiments (Table 1; LME, Expt 1, $F_{2,255} = 565.97$, p < 0.001;

Table 1. Mussel survival, length, and condition (calculated as dry weight of flesh × 100 / dry weight of shell) for both experiments for each tidal height and size class. Mussel length and condition are displayed for deployment and after 12 mo on the seabed. The mussels exposed at neap low tides in Expt 1 had no survival after 12 mo and could not be included in 12 mo length and condition data. Values are means ± SE; *denotes significant difference from deployment (p ≤ 0.05)

Expt	Shore height and size class	12 mo survival (%)	Deployment condition	12 mo condition	Deployment length (mm)	12 mo length (mm)
1	Subtidal					
	Large	76.7 ± 7.6	8.8 ± 0.5	6.4 ± 0.4 *	80.8 ± 1.8	86.5 ± 1.6
	Small	67.8 ± 3.3	6.7 ± 0.4	5.7 ± 0.4	59.1 ± 1.6	62.5 ± 1.2
	Mixed	77.3 ± 4.2	8.4 ± 0.5	5.4 ± 0.3 *	72.3 ± 3.6	80.0 ± 2.8
	Neap low tide					
	Large	0	9.5 ± 0.6	–	83.7 ± 2.6	–
	Small	0	6.7 ± 0.4	–	66.2 ± 2.6	–
	Mixed	0	8.0 ± 0.4	–	73.4 ± 3.2	–
2	Subtidal					
	Large	79.7 ± 6.3	8.7 ± 0.4	5.8 ± 0.3*	75.9 ± 2.9	89.7 ± 1.9*
	Small	70.3 ± 3.1	6.6 ± 0.3	7.7 ± 0.3	62.1 ± 1.5	71.6 ± 2.0
	Mixed	74.4 ± 2.5	8.5 ± 0.5	6.6 ± 0.3*	71.5 ± 2.6	80.6 ± 3.2
	Spring low tide					
	Large	47.2 ± 9.7	10.2 ± 0.5	4.7 ± 0.2*	85.1 ± 2.0	86.0 ± 2.0
	Small	35.5 ± 6.5	6.4 ± 0.3	6.0 ± 0.3	61.2 ± 1.4	61.7 ± 1.3
	Mixed	33.8 ± 10.0	9.7 ± 0.6	6.6 ± 0.3*	77.2 ± 2.5	73.9 ± 2.8

Expt 2, $F_{2,330} = 78.70$, p < 0.001). Also at deployment, both the large and mixed-size mussel plots had higher condition (meat vs. shell weight ratio) than the plots containing only small mussels (Table 1; LME, Expt 1, $F_{2,255} = 5.99$, p = 0.003; Expt 2, $F_{2,330} = 5.01$, p = 0.007). After 12 mo in Expt 1, only the subtidal mussels remained alive, and they had failed to grow significantly larger (LME, $F_{2,255} = 0.78$, p > 0.05). The

large and mixed-size mussels had lower condition at 12 mo compared to deployment, whereas the small mussels did not (Table 1; LME, $F_{2,255} = 0.78$, p > 0.05).

In Expt 2, mussel size class (i.e. large, small, and mixed) affected mussel condition, but shore height did not. After 12 mo, both the plots with mixed cohorts decreased in condition in both the subtidal and intertidal as compared with deployment, but the
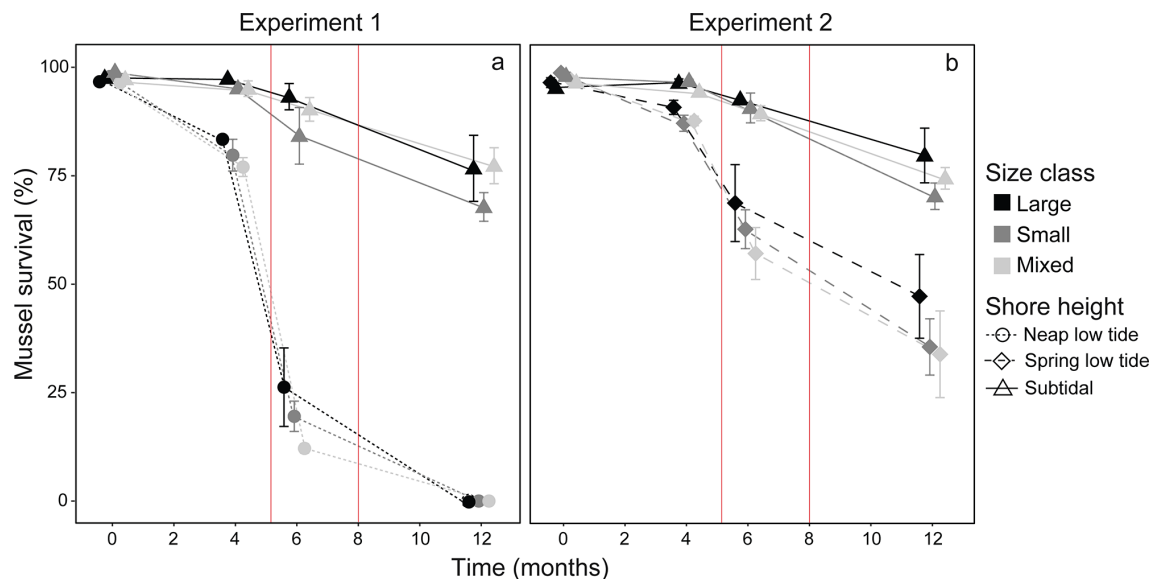

Fig. 3. Mussel survival ± SE over a 12 mo period for 2 experiments with different intertidal shore heights (Expt 1: subtidal and mussels exposed at neap low tides; Expt 2: subtidal and mussels exposed at only spring low tides) with 3 size classes (large, small, and mixed cohort). Austral summer occurs from November to February and is depicted by the red lines

small mussels did not (Table 1; LME, interactive effect, $F_{2,330} = 37.0$, p < 0.001). There were no differences in the mussel condition between the intertidal and subtidal at 12 mo (Table 1; LME, $F_{1,4} = 0.30$, p > 0.05), and only the plots containing large mussels in the subtidal increased in length (Table 1; LME, interactive effect, $F_{1,331} = 3.03$, p = 0.049).

3.3. Temperature

Mussels exposed at neap low tides in Expt 1 were exposed to air 17.2 ± 0.1 % of the time, while the mussels exposed at only spring low tides in Expt 2 were exposed for 10.6 ± 0.1 % of the time. However, mean temperatures recorded in the plots exposed at neap tides in Expt 1 were not significantly different to the mean temperatures recorded for the plots exposed only at spring low tides in Expt 2 from mid-November 2021 to mid-January 2022 (austral summer; neap low tide 19.7 ± 0.1°C, spring low tide 19.0 ± 0.1°C; pairwise Wilcoxon test p > 0.05; Fig. 4). Although the mean temperatures were not different, the longer exposure time in the mussels exposed at neap low tide in Expt 1 led to exposure to a wider range of temperatures (neap low tide 7.9 ± 0.1 to 46.2 ± 1.1°C, spring low tide 9.3 ± 0.3 to 44.7 ± 0.9°C; Fig. 4). During this 2 mo period, the mussels exposed at neap tide experienced 18 ± 5 h of extreme heat (>40°C,

Toone et al. 2023b), while the mussels exposed at only spring low tides experienced 5 ± 1 h. Recordings over 30°C were 91 ± 9 h for the mussels exposed at neap low tides and 26 ± 5 h for the mussels exposed at spring low tides.

3.4. Sea star predator abundance

Throughout the 12 mo sampling period, the predatory eleven-armed sea star was not observed in the intertidal plots in either experiment (Fig. 5). For the subtidal plots, the sea star abundance did not differ by type of mussel plot for either experiment (LME, Expt 1, $F_{2,36} = 0.02$, p > 0.05; Expt 2, $F_{2,42} = 1.19$, p > 0.05; Fig. 5). In both experiments, sea star abundance changed over time in the subtidal (LME, Expt 1, $F_{4,37} = 5.2$, p = 0.002; Expt 2, $F_{4,42} = 19.8$, p < 0.001), indicating that sea stars were moving into the plots over the 12 mo period, which was particularly evident in Expt 2 (Expt 1, deployment 0.02 ± 0.02 sea star m^{-2}; 12 mo: 0.12 ± 0.03 sea star m^{-2}; Expt 2, deployment 0.15 ± 0.06 sea star m^{-2}; 12 mo:, 1.22 ± 0.13 sea star m^{-2}; Fig. 5). Other predators observed at low tide, such as oyster catchers and predatory whelks, were low in abundance on the intertidal mussel plots at each location, but they were not systematically quantified.

4. DISCUSSION

Assessing the performance of mussels experimentally transplanted into areas where they were historically abundant provides valuable knowledge that can help to improve the outcomes of future mussel reef restoration. Historically, the upper tidal limit for wild green-lipped mussels in Pelorus Sound was mean neap high tide and, specifically in Kenepuru Sound, was around mean sea level (Flaws 1975, Fig. 1). The 3 tidal levels examined in this study (i.e. neap low tide, spring low tide, and subtidal) had different mussel survival (i.e. neap low tide ~0%, spring low tide ~39%, subtidal ~74%). The higher mortality in the intertidal plots compared to the subtidal plots was most likely due to stress associated with the regular periods of emersion during low tides (Petes et al. 2008b, Lesser 2016). These stressors associated with emersion may include exposure to intertidal predators such as oyster catchers, which were observed but not quantified in this study, lack of food, and exposure to variable air temperatures. During these low tide periods, mussels cannot feed or respire and
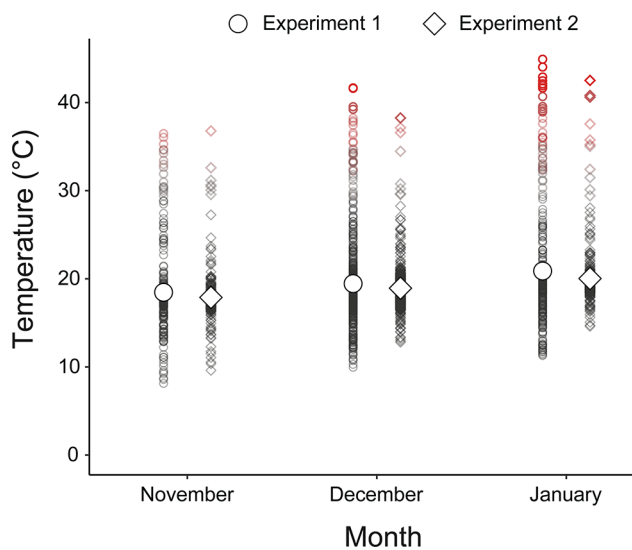

Fig. 4. Mean temperature recorded in the intertidal plots in each experiment (large symbols). In Expt 1, mussels were exposed at neap low tides, while in Expt 2, mussels were exposed at only spring low tides. Each smaller background point represents a single hourly temperature reading, with warmer temperatures emphasized in red
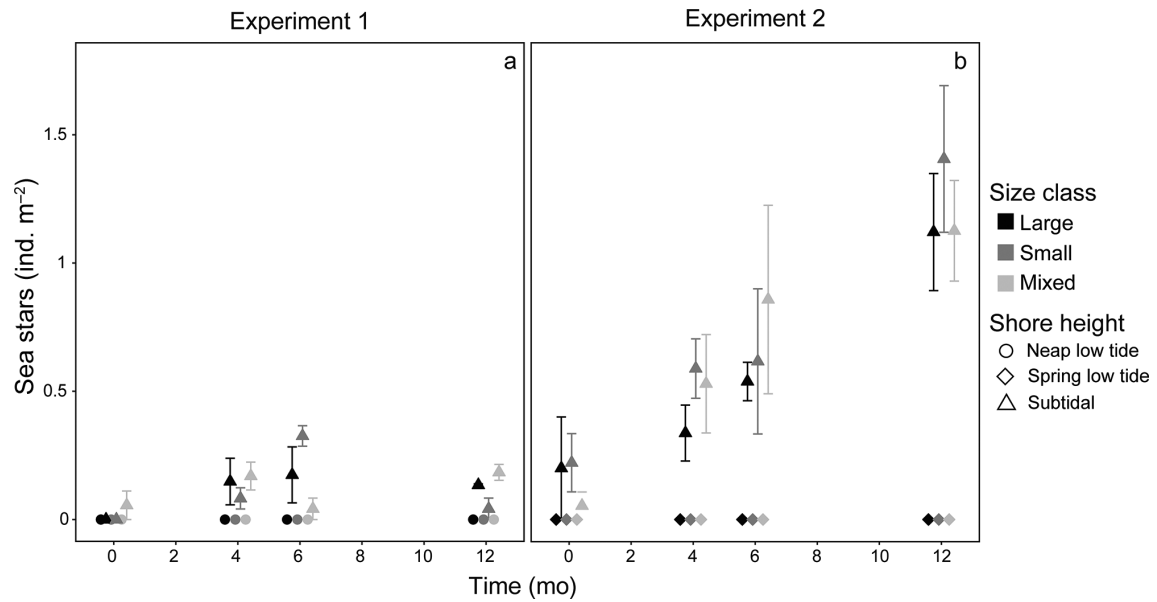
Fig. 5. Mean ± SE sea stars (ind. m^{-2}) over a 12 mo period for 2 experiments with different intertidal shore heights (Expt 1: subtidal and mussels exposed at neap low tides; Expt 2: subtidal and mussels exposed at only spring low tides) with 3 size classes of mussels (large, small, and mixed cohort)

are subject to greater temperature fluctuations and desiccation (i.e. Lesser 2016, Sorte et al. 2019). The 6 mo sampling period (January 2022) coincided with the peak of austral summer when temperatures on the shoreline during the day were higher than the ambient seawater temperature. Temperature loggers placed amongst the mussels indicated that in November 2021 through January 2022, the mussels exposed at neap low tides experienced extreme temperatures above 40°C for longer periods than the mussels exposed at only spring low tides. These months coincided with the biggest loss in mussel survival, particularly for the mussels exposed at neap low tide, which lost 61% between the October and January sampling periods.

High temperatures are known to cause oxidative heat stress and damage to cellular processes in intertidal mussels (Lesser 2006, Lesser et al. 2010, Li et al. 2020). A study on intertidal mussels on Banks Peninsula in the South Island of New Zealand found that 35% of green-lipped mussels died after an extreme heat event of 37°C in 2007 (Petes et al. 2007). Additionally, intertidal mussels collected from a range of locations around the South Island of New Zealand were experimentally exposed to emersion heat stress for 6 h, and 50% of the mussels died at 32–33°C (LT50; Sorte et al. 2019). It has been suggested that under current and future climate change conditions, green-lipped mussels will need to shift lower in the intertidal to maintain their thermal niche (Sorte et al.

2019). The 2021–2022 summer, when this current study was undertaken, was the fifth warmest summer on record in New Zealand, with above-average temperatures for the Marlborough Sounds (NIWA 2022). For mussel reef restoration, the high air temperatures and correspondingly low mussel survival when exposed at neap low tides during this study indicate that, to be viable, restoration of green-lipped mussel reefs using mussels sourced from subtidal aquaculture need to be transplanted lower in the intertidal than where mussel reefs were historically found, i.e. below spring low tide levels.

The eleven-armed sea star is a predatory sea star that has hindered mussel restoration efforts in the subtidal zone at a number of sites throughout New Zealand (Paul-Burke & Burke 2013, Wilcox & Jeffs 2019, Benjamin et al. 2022a). In the mid-Pelorus Sound, the subtidal habitat has been shown to be unsuitable for translocated mussels due to a high abundance of eleven-armed sea stars (Benjamin et al. 2023). At such locations where sea star predation is high, it is possible that the intertidal zone could be utilized for mussel restoration, as this study found no evidence of eleven-armed sea stars in the intertidal plots; however, these plots were only monitored on spring low tides. These results support findings for the Californian mussel *Mytilus californianus* in Oregon, USA, which determined that the intertidal zone was a refuge from the predatory purple sea star *Pisaster ochraceus* which cannot tolerate air expo-

sure in the mid-intertidal and is highly stressed in the low-intertidal (Petes et al. 2008a). In the current study, sea stars were recorded in the subtidal zone only where they may have contributed to some mussel mortality, but in low numbers compared to other subtidal mussel reef restoration initiatives in New Zealand (Wilcox & Jeffs 2019, Benjamin et al. 2022b). Additionally, there was no evidence of size-based prey preference, as the sea star abundance recorded between the 2 size classes or mixed cohorts of mussels in either experiment was not significantly different. Optimal foraging theory of ecology indicates that predators will choose the prey with the highest amount of nutritional return (Emlen 1966), and a study performed in a laboratory setting indicated that the eleven-armed sea star preferentially sought out green-lipped mussels sized 30–80 mm compared to 8–20 mm (Wilcox & Jeffs 2019). In a study in the Netherlands, the opposite was shown to be true for the sea star *Asterias rubens* and its blue mussel *Mytilus edulis* prey, where smaller mussels were preferentially chosen over potentially more nutritionally rewarding larger mussels (Hummel et al. 2011). The low sea star numbers and relatively small size difference of mussels tested in this study, however, suggest that more research is required to evaluate sea star predation as a limitation to using small mussels in subtidal mussel restoration.

When smaller mussels are used for restoration, it reduces transport costs, as more mussels are transported per tonne, compared to larger mussels. Smaller mussels also have the potential as they grow to form and occupy a larger restored mussel reef area. This study confirms that at optimal intertidal and subtidal levels, smaller mussels can be used without lowering translocation success (i.e. mussel survival). However, the survival threshold may differ for mussels smaller than the size tested in this study, but for factors other than heat stress or sea star predation. For example, a study in the North Island, New Zealand, reported that smaller green-lipped mussels (i.e. <30 mm) need to be protected from mobile fish predators (Alder et al. 2021a). Additionally, when *M. edulis* mussel seed are transplanted to the seafloor, even with predator protection, there can be high losses both in the intertidal from wave action (Schotanus et al. 2020b) and in the subtidal from handling stress (Capelle et al. 2016). In the present study, 60 mm mussels were successfully transplanted in the subtidal and intertidal zones without predator protection. This is likely due to the high deployment densities (e.g. Benjamin et al. 2023), selection of locations with minimal natural predators (e.g. Benjamin

et al. 2023), and the relatively large size of the mussels compared to other studies (i.e. Alder et al. 2021a). However, as a 25% reduction in size class resulted in 50% more mussels being deployed, it is recommended that the optimum size for success of green-lipped mussel transplantation is further evaluated across multiple locations.

There were no juvenile mussel recruits visually detected in any of the restored mussel plots in this study. Although recruitment is critical to the long-term success of a restored mussel reef, the lack of observed recruitment is common for mussel restoration efforts in this study area and in other parts of New Zealand (Wilcox et al. 2018, Benjamin et al. 2022b, 2023, Toone et al. 2023b). However, this study area does not appear to be limited by larval supply, as active mussel settlement upon settlement collectors has been consistent over 4 decades (Toone et al. 2022). There are new approaches being developed in the Netherlands and USA to incorporate life cycle aspects to restoration methodologies which have been shown to overcome barriers in the early stages of the mussel lifecycle (Temmink et al. 2021). It is possible that these life-cycle informed methodologies may need to be considered for mussel restoration in New Zealand to identify and overcome barriers to mussel recruitment and increase the long-term viability of the restored mussel reefs. Additionally, this study occurred over the course of 1 yr, which is within the timeframe recommended by global shellfish guidelines to develop and monitor pilot restoration studies (i.e. 1–3 yr; Fitzsimons et al. 2020), but is early to determine and draw conclusions about long-term results. It is possible that the shorter timeframe may also be responsible for the lack of juvenile recruitment, as oyster reef restoration has determined it takes 3 yr for a restored reefs to attract oyster recruits and produce broodstock (Smith et al. 2022).

This study demonstrates the viability of transplanting smaller mussels (60 mm) as a lower cost option with greater areal restoration potential compared to deploying larger mussels (80 mm) in the shallow intertidal and subtidal zones. The upper limit in the intertidal zone for the survival of green-lipped mussels appears to be controlled by tidal height affecting extreme heat exposure times, whereas predation by sea stars appears to control subtidal restoration survival. The intertidal results suggest that exposure time needs to be minimised to maximise survival, particularly in the face of increasing summer temperatures due to climate change. Using green-lipped mussels sourced from aquaculture for restoration in

the upper tidal limits where wild mussels were historically found appears currently unviable. These results have important implications for increasing mussel restoration success in New Zealand and informing shellfish restoration efforts globally with climate change, as historical species distributions will likely become unsuitable restoration habitats for transplanting animals from aquaculture.

LITERATURE CITED

Alder A, Jeffs A, Hillman JR (2021a) Considering the use of subadult and juvenile mussels for mussel reef restoration. Restor Ecol 29:e13332

Alder A, Jeffs AG, Hillman JR (2021b) The importance of stock selection for improving transplantation efficiency. Restor Ecol 30:e13561

Andrade M, De Marchi L, Soares AMVM, Rocha RJM, Figueira E, Freitas R (2019) Are the effects induced by increased temperature enhanced in *Mytilus galloprovincialis* submitted to air exposure? Sci Total Environ 647: 431–440

Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67: 1–42

Bayraktarov E, Saunders MI, Abdullah S, Mills M and others (2016) The cost and feasibility of marine coastal restoration. Ecol Appl 26:1055–1074

Bayraktarov E, Brisbane S, Hagger V, Smith CS and others (2020) Priorities and motivations of marine coastal restoration research. Front Mar Sci 7:484

Beck MW, Brumbaugh RD, Airoldi L, Carranza A and others (2009) Shellfish reefs at risk: a global analysis of problems and solutions. The Nature Conservancy, Arlington, VA

Beck MW, Brumbaugh RD, Airoldi L, Carranza A and others (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. BioScience 61: 107–116

Benjamin ED, Handley SJ, Hale R, Toone TA, Jeffs A, Hillman JR (2022a) Biodiversity associated with restored small-scale mussel habitats has restoration decision implications. Biodivers Conserv 31:2833–2855

Benjamin ED, Hillman JR, Handley SJ, Toone TA, Jeffs A (2022b) The effectiveness of providing shell substrate for the restoration of adult mussel reefs. Sustainability 14: 15746

Benjamin ED, Handley SJ, Jeffs A, Olsen L, Toone TA, Hillman JR (2023) Testing habitat suitability for shellfish restoration with small-scale pilot experiments. Conserv Sci Pract 5:e12878

Bertolini C, Montgomery WI, O'Connor NE (2018) Habitat with small inter-structural spaces promotes mussel survival and reef generation. Mar Biol 165:163

Capelle JJ, Scheiberlich G, Wijsman JWM, Smaal AC (2016) The role of shore crabs and mussel density in mussel losses at a commercial intertidal mussel plot after seeding. Aquacult Int 24:1459–1472

Capelle JJ, Leuchter L, de Wit M, et al (2019) Creating a window of opportunity for establishing ecosystem engineers by adding substratum: a case study on mussels. Ecosphere 10:e02688

Commito JA, Como S, Grupe BM, Dow WE (2008) Species diversity in the soft-bottom intertidal zone: biogenic structure, sediment, and macrofauna across mussel bed spatial scales. J Exp Mar Biol Ecol 366:70–81

de Paoli H, van de Koppel J, van der Zee E, Kangeri A and others (2015) Processes limiting mussel bed restoration in the Wadden-Sea. J Sea Res 103:42–49

de Paoli H, van der Heide T, van den Berg A, Silliman BR, Herman PMJ, van de Koppel J (2017) Behavioral self-organization underlies the resilience of a coastal ecosystem. Proc Natl Acad Sci USA 114:8035–8040

Emlen JM (1966) The role of time and energy in food preference. Am Nat 100:611–617

Fitzsimons J, Branigan S, Brumbaugh RD, McDonald T, zu Ermgassen SE (eds) (2019) Restoration guidelines for shellfish reefs. The Nature Conservancy, Arlington, VA

Fitzsimons JA, Branigan S, Gillies CL, Brumbaugh RD and others (2020) Restoring shellfish reefs: global guidelines for practitioners and scientists. Conserv Sci Pract 2:e198

Flaws DE (1975) Aspects of the biology of mussels in the Cook Strait Area. PhD thesis, Victoria University, Wellington

Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. Sage, Thousand Oaks, CA

Frandsen R, Dolmer P (2002) Effects of substrate type on growth and mortality of blue mussels (*Mytilus edulis*) exposed to the predator *Carcinus maenas.* Mar Biol 141: 253–262

Hawkins AJS, James MR, Hickman RW, Hatton S, Weatherhead M (1999) Modelling of suspension-feeding and growth in the green-lipped mussel *Perna canaliculus* exposed to natural and experimental variations of seston availability in the Marlborough Sounds, New Zealand. Mar Ecol Prog Ser 191:217–232

Hickman RW (1979) Allometry and growth of the green-lipped mussel *Perna canaliculus* in New Zealand. Mar Biol 51:311–327

Hillman JR, O'Meara TA, Lohrer AM, Thrush SF (2021) Influence of restored mussel reefs on denitrification in marine sediments. J Sea Res 175:102099

Hummel C, Honkoop P, van der Meer J (2011) Small is profitable: no support for the optimal foraging theory in sea stars *Asterias rubens* foraging on the blue edible mussel *Mytilus edulis.* Estuar Coast Shelf Sci 94:89–92

Jeffs A, Holland R, Hooker S, Hayden B (1999) Overview and bibliography of research on the greenshell mussel, *Perna canaliculus*, from New Zealand waters. J Shellfish Res 18:347–360

Lenth RV (2018) Emmeans: estimated marginal means. http://cran.nexr.com/web/packages/emmeans/emmeans.pdf

Lesser MP (2006) Oxidative stress in marine environments: biochemistry and physiological ecology. Annu Rev Physiol 68:253–278

Lesser MP (2016) Climate change stressors cause metabolic depression in the blue mussel, *Mytilus edulis*, from the Gulf of Maine. Limnol Oceanogr 61:1705–1717

Lesser MP, Bailey MA, Merselis DG, Morrison JR (2010) Physiological response of the blue mussel *Mytilus edulis* to differences in food and temperature in the Gulf of Maine. Comp Biochem Physiol A Mol Integr Physiol 156: 541–551

Li S, Alfaro AC, Nguyen TV, Young T, Lulijwa R (2020) An integrated omics approach to investigate summer mortality of New Zealand Greenshell™ mussels. Metabolomics 16: 100

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH and others (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809

Lucas A, Beninger PG (1985) The use of physiological condition indices in marine bivalve aquaculture. Aquaculture 44:187–200

Menge BA, Daley BA, Sanford E, Dahlhoff EP, Lubchenco J (2007) Mussel zonation in New Zealand: an integrative eco-physiological approach. Mar Ecol Prog Ser 345: 129–140

Newell R (2004) Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. J Shellfish Res 23:51–61

NIWA (National Institute for Water and Atmospheric Research) (2022) Seasonal climate summary: summer 2021–2022. NIWA, Wellington

Paul LJ (2012) A history of the Firth of Thames dredge fishery for mussels: use and abuse of a coastal resource. New Zealand Aquatic Environment Biodiversity Rep No. 94. NIWA, Wellington

Paul-Burke K, Burke J (2013) Monitoring assessment of kūtai (*Perna canaliculus*) green-lipped mussel and pātangaroa (*Coscinasterias muricata*) seastar populations in the western side of Ōhiwa Harbour 2013. Tech Rep. Te Rūnanga o Ngāti Awa, Whakatāne

Paul-Burke K, Ngarimu-Cameron R, Burke J, Bulmer R and others (2022) Taura kuku: prioritising Māori knowledge and resources to create biodegradable mussel spat settlement lines for shellfish restoration in Ōhiwa harbour. NZ J Mar Freshw Res 56:570–584

Petes LE, Menge BA, Murphy GD (2007) Environmental stress decreases survival, growth, and reproduction in New Zealand mussels. J Exp Mar Biol Ecol 351:83–91

Petes LE, Menge BA, Harris AL (2008a) Intertidal mussels exhibit energetic trade-offs between reproduction and stress resistance. Ecol Monogr 78:387–402

Petes LE, Mouchka ME, Milston-Clements RH, Momoda TS, Menge BA (2008b) Effects of environmental stress on intertidal mussels and their sea star predators. Oecologia 156:671–680

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Schotanus J, Capelle JJ, Leuchter L, van de Koppel J,

Bouma TJ (2019) Mussel seed is highly plastic to settling conditions: the influence of waves versus tidal emergence. Mar Ecol Prog Ser 624:77–87

Schotanus J, Capelle JJ, Paree E, Fivash GS, van de Koppel J, Bouma TJ (2020a) Restoring mussel beds in highly dynamic environments by lowering environmental stressors. Restor Ecol 28:1124–1134

Schotanus J, Walles B, Capelle JJ, van Belzen J, van de Koppel J, Bouma TJ (2020b) Promoting self-facilitating feedback processes in coastal ecosystem engineers to increase restoration success: testing engineering measures. J Appl Ecol 57:1958–1968

Sea MA, Thrush SF, Hillman JR (2021) Environmental predictors of sediment denitrification rates within restored green-lipped mussel *Perna canaliculus* beds. Mar Ecol Prog Ser 667:1–13

Sea MA, Hillman JR, Thrush SF (2022) Enhancing multiple scales of seafloor biodiversity with mussel restoration. Sci Rep 12:5027

Smith RS, Lusk B, Castorani MCN (2022) Restored oyster reefs match multiple functions of natural reefs within a decade. Conserv Lett 15:e12883

Sorte CJB, Davidson VE, Franklin MC, Benes KM and others (2017) Long-term declines in an intertidal foundation species parallel shifts in community composition. Glob Change Biol 23:341–352

Sorte CJB, Bernatchez G, Mislan KAS, Pandori LLM, Silbiger NJ, Wallingford PD (2019) Thermal tolerance limits as indicators of current and future intertidal zonation patterns in a diverse mussel guild. Mar Biol 166:6

Stead DH (1969) Pelorus Sound: mussel survey December 1969. Fish Tech Rep 62. Fisheries Division, Marine Department, Wellington

Temmink RJM, Angelini C, Fivash GS, Swart L and others (2021) Life cycle informed restoration: engineering settlement substrate material characteristics and structural complexity for reef formation. J Appl Ecol 58:2158–2170

Toone TA, Hunter R, Benjamin ED, Handley S, Jeffs A, Hillman JR (2021) Conserving shellfish reefs — a systematic review reveals the need to broaden research efforts. Restor Ecol 29:e13375

Toone TA, Benjamin ED, Handley S, Jeffs A, Hillman JR (2022) Expansion of shellfish aquaculture has no impact on settlement rates. Aquacult Environ Interact 14:135–145

Toone TA, Benjamin ED, Hillman JR, Handley S, Jeffs A (2023a) Multidisciplinary baselines quantify a drastic decline of mussel reefs and reveal an absence of natural recovery. Ecosphere 14:e4390

Toone T, Hillman JR, Benjamin ED, Handley S, Jeffs A (2023b) Out of their depth: the successful use of cultured subtidal mussels for intertidal restoration. Conserv Sci Pract 5:e12914

Wentworth CK (1922) A scale of grade and class terms for clastic sediments. J Geol 30:377–392

Wilcox M, Jeffs A (2019) Impacts of sea star predation on mussel bed restoration. Restor Ecol 27:189–197

Wilcox M, Kelly S, Jeffs A (2018) Ecological restoration of mussel beds onto soft-sediment using transplanted adults. Restor Ecol 26:581–590