Effects of suspended sediment on survival, growth, and nutritional condition of green-lipped mussel spat (*Perna canaliculus,* Gmelin, 1791)

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ABSTRACT

Suspended sediment is a significant current threat to coastal ecosystems in many parts of the world. Sediment runoff into the ocean is increasing due to numerous human activities, such as agriculture, deforestation, construction, and mining. Additionally, climate change is impacting local weather patterns, with many regions experiencing marked changes in the frequency and extent of precipitation. Extreme weather events, such as cyclones, can increase suspended sediment (SS) in coastal waters by up to 100-fold. This rapid change in SS can negatively affect filter-feeding bivalves by diminishing their feeding efficiency, often preventing feeding until the sediment settles. In New Zealand, juveniles of the green-lipped mussel (*Perna canaliculus*) have rudimentary structures for capturing and sorting food particles from the seston, which are prone to clogging and damage. In this study, the effects of a range of SS concentrations (0–1250 mg L^{-1}) on the survival, growth, and nutritional condition of juvenile green-lipped mussels (1–2 mm SL) were determined over two time scales (5 and 30 days) in controlled laboratory experiments. Neither mortality nor nutritional condition were impacted by SS. However, the presence of SS positively affected growth ($p < 0.05$) and mussel settlement location ($p < 0.01$) at both time scales. The results show that, under these conditions, SS levels $\leq$1250 mg L^{-1} are not apparently harmful to *P. canaliculus* spat and may even be advantageous.

1. Introduction

Elevated suspended sediment (SS) in coastal waters is increasingly recognised as a significant ecological threat to aquatic species, especially suspension feeders (Ellis et al., 2002; Lohrer et al., 2006; Lummer et al., 2016). Suspended sediment in coastal waters originates from the erosion and dispersal of terrestrial sediment and can be altered by several natural factors, including tectonic activity, lithology, precipitation, and vegetation (Hicks et al., 1996, 2011; Trustrum et al., 1999). Mountainous Southwest Pacific islands are particularly prone to erosion due to their high ocean exposure, frequent tectonism and volcanism, mountainous terrain, young and erodible rock, periodic intense rainfall and weather events (e.g., cyclones, orographic induced rainfall), and short drainage basins (Gayer et al., 2019; Goldsmith et al., 2008; Kao and Liu, 2002; Milliman and Meade, 1983; Pariyar et al., 2020). These islands have some of the highest global weathering and erosion rates, collectively contributing >30 % of the global annual ocean sediment yield (Carey et al., 2002; Hicks et al., 1996, 2011; Meyer et al., 2017; Milliman et al., 1999). Human colonisation additionally exacerbates this

high erosion with urban development, agriculture, mining, and deforestation (McLeod et al., 2011; Milliman et al., 1999; Paul, 2012).

Many Southwest Pacific islands have been severely deforested (Nunn, 1990; Rolette and Diamond, 2004). Easter Island, for example, was entirely deforested by the prehistoric Rapanui civilisation (Rull, 2020; but see Davis et al., 2024), while substantial native vegetation has also been cleared in New Zealand (Adams, 1979; Gomez et al., 2009; Hicks et al., 2011; Rolett and Diamond, 2004; Rull, 2020; Selby, 1972). Deforestation leads to slope instability and soil loss (Nunn, 1990), increasing sediment runoff yields by up to 10 times (2–3 times on average; Hicks et al., 2011; Milliman and Meade, 1983; Milliman and Syvitski, 1992). Many Southwest Pacific islands are also highly vulnerable to climate change, as increased frequency and intensity of rainfall, floods, monsoons, and cyclones are all projected for their future (IPCC, 2023; Pariyar et al., 2020). Cyclones and intense precipitation can trigger high erosion events, such as landslides and floods (Gayer et al., 2019). For example, Typhoon Mindulle deposited 61 million t of sediment into the Choshui River in Taiwan (Goldsmith et al., 2008), while in New Zealand, SS in estuaries typically increases from 10 to 1000 mg L^{-1}

during large storms (Ellis et al., 2002; Hewitt and Norkko, 2007). Hence, human activities substantially impact erosion, increasing sediment runoff to the ocean.

Extreme sediment fluxes threaten estuarine and coastal filter-feeding organisms, such as bivalves, by rapidly and dramatically increasing SS levels. This leaves organisms little time to respond, leading to burial, suffocation, and starvation (Poirier et al., 2021). High SS levels pose a significant threat to filter-feeding bivalves (Safi et al., 2007), but the level that triggers a response and the type of response depends on numerous factors, including the bivalve species (Safi et al., 2007; Ward and MacDonald, 1996), their adaptability (Lohrer et al., 2006; Tuttle-Raycraft and Ackerman, 2019), exposure characteristics (Grant and Thorpe, 1991; Hewitt and Norkko, 2007), and SS quality (Tuttle-Ray-craft and Ackerman, 2018; Ward and MacDonald, 1996). Stressors like SS may also have life-stage-specific impacts due to ontological differences in lifestyle (e.g., sessile/planktonic, benthic/pelagic) and feeding (e.g., morphology, diet). For example, the responses of three different freshwater mussels (*Lampsilis fasciola, Lampsilis siliquoidea,* and *Sagittunio nasuta*) varied markedly by life stage when exposed to elevated SS, with clearance rates increasing in the 1-week-old mussels and decreasing in older juveniles and adults (Tuttle-Raycraft et al., 2017). It is commonly recognised that younger life stages of marine invertebrates are less tolerant of environmental stressors than adults (Chelyadina et al., 2017; Ringwood, 1993). However, the life stage studies that support these claims are less common and primarily relate to heavy metal stressors and not SS (Calabrese et al., 1973; Connor, 1972; Markich, 2021; Martin et al., 1981; Ringwood, 1993). Meanwhile, studies that are focused on SS have found variable results. For example, *Pinna nobilis* and *Mercenaria mercenaria* juvenile growth (length and weight) were negatively affected by SS (Acarli et al., 2011; Bricelj and Malouf, 1984), while *Limnoperna fortunei* larval growth was positively affected (Eilers et al., 2011), and *Corbicula fluminea* growth was unaffected (Foe and Knight, 1985). Moreover, *Crassostrea virginica* juveniles were less abundant in high turbidity (Reustle and Smee, 2020), and *Dreissena polymorpha* veligers were more abundant in high turbidity (Barnard et al., 2003); however, neither study characterised the suspended particles in the water column. Therefore, the specific impacts of increased SS on bivalves vary and are challenging to predict.

Bivalve settlement and recruitment may also be negatively affected by high SS concentrations, disrupting settlement cues (e.g., chemical and light), reducing oxygen availability, or coating settlement substrates, making them unfavourable or difficult to settle on (Poirier et al., 2021). For example, *C. virginica* recruitment is negatively affected by sediment stress (Thomsen and McGlathery, 2006) and high turbidity (Reustle and Smee, 2020), and juvenile *Margaritifera margaritifera* presence is correlated with turbidity and inorganic sedimentation (Österling et al., 2010). Restoration of wild mussel populations in New Zealand has been limited by recruitment, with no recruits observed in over a year in South Island restoration projects (Benjamin et al., 2022, 2023; Toone et al., 2023) and only three recruiting individuals found within 2 years in a North Island study (Wilcox et al., 2018). This lack of recruitment suggests an unfavourable environment for recruitment, with SS implicated as a likely reason due to dramatic increases in sediment discharge in these coastal regions (Handley et al., 2017; Swales et al., 2016). In green-lipped mussel (*Perna canaliculus*) early juveniles, the filter-feeding structures are not fully developed, have lower particle capture efficiency and a reduced ability to sort particles compared to adults, and are prone to blockage and damage (Gui et al., 2016a, 2016b). Elevated mortality, reduced growth, and lack of settlement could be expected when juvenile green-lipped mussels are exposed to elevated SS because of the increased energy requirements needed to filter sufficient food particles due to reduced feeding efficiency. For example, low green-lipped mussel settlement near the seafloor has been associated with high turbidity (Toone et al., 2023). To determine whether high SS is limiting mussel recruitment in New Zealand, the current study explores the effects of a range of suspended sediment concentrations on the survival, growth, and nutritional condition of *P. canaliculus* early juveniles.

2. Methods

2.1. Mussel collection and acclimatisation

The experiments in this study used hatchery-reared, green-lipped mussel early juveniles, commonly known as spat. The spat were supplied by a commercial mussel hatchery (SPATnz Ltd. Nelson, New Zealand) in two batches (May 2023 and March 2024) as plantigrades of ~1–2 mm mean shell length (SL), approximately one-month post-metamorphosis. The hatchery utilises a continuous-flow seawater system at 20 °C, with seawater filtered to 1 μm and treated with UV.

After transport to the seawater facilities at the University of Auckland's School of Biological Sciences, mussel spat were added freely to the water column of 20 L tanks in 18 °C filtered and sterilised seawater (FSW) with constant aeration in a temperature-controlled laboratory.

2.2. Mussel husbandry

Before experimentation, mussels were acclimatised for 1 week. During this period, FSW was replaced in 20 L holding tanks every second day. Tanks were rinsed thoroughly with freshwater once per week to reduce bacterial load; mussels were gently detached from tank walls with a soft bottle brush, gently poured over a 200 μm sieve, rinsed, and returned to the tank with FSW. Mussels were fed one species of laboratory-cultured axenic microalgae (i.e., *Tisochrysis lutea, Nannochloris atomus, Chaetoceros muelleri,* and *Diacronema lutheri*) in rotation at ~500,000 cells mussel^{-1} day^{-1} (concentration determined by Muse® Cell Analyser, Millipore Sigma), which is sufficient to meet their nutritional requirements to support growth (Sanjayasari and Jeffs, 2019).

2.3. Sediment collection and preparation

Surface benthic sediment was collected from a mudflat in the inner Whangateau Harbour, New Zealand, which was chosen based on ease of collection and low heavy metal contamination (Allen, 2023). Sediment was defaunated with a 200 μm sieve. The silt/clay-sized fraction of the sediment was then separated with a 63 μm sieve and retained, as particles larger than this were known to clog filter-feeding structures in the mussel spat based on previous research (Gui et al., 2016a). Sediment was thoroughly rinsed with freshwater to remove any soluble fraction that could interfere with results. To retain the natural characteristics of the sediment, it was not further sterilised and was refrigerated until use.

To determine reliable concentrations of suspended sediment in seawater, the relationships among the mass of dried sediment in suspension, the mass of wet sediment in suspension, and turbidity measurements were established for nine suspended sediment concentrations between 0 and 700 mg L^{-1}. The nine concentrations were created by adding different masses of wet sediment (ThermoFisher Scientific Sartorius LE2445 analytic scale) from the stock sediment source to 500 mL of FSW in lidded 1 L Schott bottles. Sediments were maintained in suspension by vigorous shaking, and the bottles were then placed on a stir plate with a magnetic stir bar inside the bottle for 10 min. The suspended sediment turbidity was determined by three replicate readings with a YSI ProDSS Swap turbidity meter (Xylem, Yellow Springs, Ohio). To determine the dry sediment mass of each solution, the bottles were re-inverted, and three replicate 25 mL samples were filtered with a Terumo 50 mL syringe through a dried Whatman binder-free glass microfibre filter (25 mm diameter, 0.7 μm particle retention). The syringes were rinsed of remaining particles and salt with 10 mL of Milli-Q water. Filters were oven-dried at 60 °C for 48 h and re-weighed. The line-of-best-fit equation was determined by calibration curves for the relationships among the corresponding sediment dry weight of the solutions with sediment wet weight and turbidity measurements (Supplementary Fig. S1).

2.4. Acute SS exposure experiment

Acute effects of suspended sediment on mussel spat were determined in a 5 day experiment conducted at a range of SS exposure levels. A series of ten exponentially increasing SS concentrations (0, 5, 10, 25, 50, 100, 250, 500, 1000, 1250 mg L^{-1} dry mass sediment) was used for a dose–response experiment with the <63 μm wet-sieved sediment in 1.5 L conical tanks (Supplementary Table S1). To maintain dissolved oxygen and keep sediment homogeneously suspended, an airstone was sealed into the base of the conical tank and connected to an aquarium air pump. A 10 × 15 cm plastic mesh strip (1 mm mesh size) was suspended in each tank by nylon thread as an attachment substrate for the mussels (Supplementary Fig. S2).

For each tank, 50 green-lipped mussel spat (0.39–4.37 mm SL; mean 1.91 mm) were haphazardly selected from the stock supply, photographed to determine SL at the outset (using image analyses), and added freely to the water column of a randomly selected 1.5 L tank.

The wet sediment mass required for each SS treatment was calculated based on the calibration curve (Supplementary Fig. S1). Wet sediment was weighed and mixed thoroughly into 100 mL FSW before being added to the conical tanks holding 900 mL of FSW. After the SS was added, turbidity was measured with a YSI ProDSS Swap meter (Xylem Inc., Yellow Springs, Ohio) and again 1 h later to ensure sediments remained in suspension. Temperature and salinity were measured twice daily in each tank with a Professional Plus YSI Model 30 (Xylem Inc., Yellow Springs, Ohio), as was oxygen with a Hach HQ40d Luminescent Dissolved Oxygen Probe Model LDO101.

The FSW was changed daily by gently pouring tank contents over a 200 μm sieve to retain unattached spat. The tanks and mussels were gently rinsed with freshwater to reduce surface bacteria without dislodging attached mussels. Then, loose mussels were returned to the tank, followed by fresh sediment solution (as described above) and the cultured microalgae diet. The mussels were fed a rotation of four cultured microalgae species, as described above.

At the end of the 5 days, the mussel attachment location in each tank was noted (i.e., either on the mesh or the tank bottom) and recorded. Spat were then carefully removed from the tanks, and every mussel was determined to be living or dead, counted under a dissection microscope, and photographed to obtain experiment end SL measurements using ImageJ Software (Rasband, 2011). Spat were considered dead if the shells were visibly empty or there was no sign of foot, gill, or valve (opening) movement for 30 min. Some mussels were accidentally lost during water changes, so the total final number of mussels per tank was lower than the initial number. Percent mortality was calculated for each tank as the number of mussels that were verified dead divided by the total final remaining mussels (dead + alive) × 100 %.

2.5. Chronic SS exposure experiment

To determine the chronic effects of SS on mussel spat, a 30 day experiment was conducted at five exposure levels of dry sediment mass (0, 10, 100, 1000, 1250 mg L^{-1}), each with five replicates and 1 g (~ 1300 individuals) of green-lipped mussel spat per tank. Based on the results of the previous experiment, eight treatments within 0–1000 mg L^{-1} were deemed unnecessary, so fewer concentrations were utilised while maintaining the same overall range (0–1250 mg L^{-1}). The tanks, suspended sediment procedure, daily maintenance, feeding, and physical measurements were the same as described above for the acute SS exposure experiment. However, turbidity was not measured 1 h after adding SS, as it was deemed unnecessary based on the previous experiment. Additionally, to analyse sediment characteristics at the end of the experiment, the water was collected from daily water changes, retained, and decanted to recover the sediment ("recovered sediment" from all treatments pooled).

The number of mussels in 1.0 g (wet weight) was determined before the experiment by counting the number of spat in ten 0.1 g samples and then calculating the mean number per gram (i.e., 1329 ± 104 (SE) individuals g^{-1}). The average number of individuals per tank was only calculated as a reference; it was not used in any statistical analyses.

The green-lipped mussel spat (0.31–2.71 mm SL; mean 1.35 mm) were haphazardly selected from the holding tank and weighed to 1.0 g. Three randomly selected sub-samples of 50 mussels per tank were photographed to determine the mean SL at outset. Then, the entire 1.0 g of mussels was added freely to the water column of one randomly selected tank. This process was repeated for each tank.

At the end of 30 days, the location of final spat attachment was recorded and photographed, and then they were carefully removed from the tanks. Every mussel was sorted into living and dead (as described above) under a dissection microscope, counted to determine mortality, and photographed to obtain experiment end SL measurements. Afterward, spat were rinsed in freshwater and frozen until further processing. The experiment end SL of all mussels (i.e., both alive and dead) were measured from photographs using ImageJ Software (Rasband, 2011).

Spat dry weight was determined by lyophilizing (Christ Alpha 2–4 LSC, Buch & Holm A/S, Herlev, Denmark) all frozen spat for 24 h. The ash-free dry weight (AFDW) of spat was determined by ashing three ~0.1 g samples per tank of lyophilized mussels (*n* = 75 samples: 3 replicates × 5 tanks per treatment level × 5 treatment levels) for 5 h at 450 °C (Nabertherm LT15/11/B410 muffle furnace, Germany). The total organic matter (TOM, %) of mussel samples was calculated as (AFDW/total dry weight of sample) × 100 %.

The calorific content per gram of dry mussel was determined using three ~0.2 g samples per tank of lyophilized spat (*n* = 75 samples: 3 replicates × 5 tanks per treatment level × 5 treatment levels) (Parr 6725 semimicro calorimeter, Parr Instrument Company, USA). This was converted to calorific content per gram of organic matter using the percent TOM calculated above for each SS treatment (Supono et al., 2020). Calorific content, AFDW, and TOM were determined using a mixture of mussels from different settlement locations within each tank. The minimum soft tissue requirements to measure calorific content were too high to allow the separate analysis of mussels per settlement location.

2.6. Sediment analyses

The AFDW of stock and recovered sediments from the chronic SS experiment was determined by lyophilizing nine replicate 0.1 g samples of each for 24 h, weighing, and then ashing in a muffle furnace at 450 °C for 5 h. The total organic matter (TOM, %) of the sediment samples was then calculated as (AFDW/total dry weight of sample) × 100 %. The grain size distribution of stock and recovered sediments was determined by adding 40 mL hydrogen peroxide to 15 mL of sediment for 7 days to dissolve the organic material. Then, samples were centrifuged and rinsed with deionised water three times, and 10 mL Calgon was added to each sample to break up particle aggregates before processing with a Malvern Mastersizer 3000 (ATA Scientific).

2.7. Statistical analyses

All data analyses and presentations were conducted with RStudio v4.3.0 (Posit Team, 2023). In all cases, *p*-values <0.05 were considered statistically significant. The two experiments (short and long term) were analysed separately using linear mixed-effects models (lme4::lmer; Bates et al., 2015) and generalised linear mixed-effects models (lme::glmer). Where models were significant, contrasts were computed with the estimated marginal means package (emmeans; Searle et al., 1980) for factor-level comparisons.

Mortality analyses used a generalised model to specify the family as binomial (0 = dead, 1 = alive), and tank was included as a random intercept effect to account for the non-independence of mussels within a tank. Settlement location was analysed similarly, with a binomial glmer (0 = bottom of tank, 1 = mesh), and tank was included as a random

effect.

Mussel growth analyses used an lmer model. All of the measured mussel lengths were included: for the short term experiment, $n = 946$ (~50 mussels × 10 tanks × 2 time points); for the long-term experiment, $n = 29{,}268$ (~250 mussels × 25 tanks at outset and ~1000 mussels × 25 tanks at end). To account for the non-independence of mussels within a tank, a random intercept effect was included. Time (experiment outset vs. experiment end) was included as an explanatory fixed effect to explore the difference in mussel SL through time. Growth was also tested between mussel settlement locations (long-term experiment only), using the same model structure with settlement location included as a fixed effect. Only the SL data from the experiment end were used for this analysis, so time was not included. As above, tank was included as a random effect.

The lmer model was also used to test for differences in TOM and calorific content. Time was not included, as the TOM/calorific content data from experiment outset were not sufficient for comparison. The models for the above analyses, as coded in r, are shown below.

glmer(Mortality [or Settlement] ~ SS_Treatment + (1 | Tank), family = Binomial, data = df)

lmer(Length ~ SS_Treatment*Time + (1 | Tank), data = df)

lmer(Length ~ SS_Treatment*Settlement_Location + (1| Tank), data = df)

lmer(TOM [or Calorific_Content] ~ SS_Treatment + (1 | Tank), data = df)

Differences in physical parameters (temperature, oxygen, salinity) among tanks were tested separately with two-way repeated-measures ANOVA to determine whether any differences may have impacted the results. None of the physical parameters had significant differences among tanks for the short-term experiment, so they were not expected to impact the results and were not included in the final explanatory models (Supplementary Fig. S3). Temperature and oxygen were not significantly different among tanks in the long-term experiment and did not impact the results of models, and therefore, were not included in the final explanatory models for the long-term experiment (Supplementary Figs. S4, S5). Salinity was significantly different among tanks, so it was initially included in the model, however, it had no impact on the model result and was subsequently removed (Supplementary Fig. S6).

Statistical analyses were not possible for the sediment analyses due to the way the recovered sediments were collected (all SS treatment levels pooled, no controls).

3. Results

3.1. Acute SS exposure experiment

Mussel spat mortality was relatively low for all treatments (range = 4–13 %; mean = 8 %) and was not affected by SS treatment ($p = 0.668$; Fig. 1A, Table S2).

Mean mussel spat shell lengths (SLs) were 0.39–4.37 mm (mean = 1.91 mm) at the outset and 0.96–4.56 mm (mean = 2.06 mm) at the end of the acute exposure experiment. In the linear model, SL was related to time (outset versus end; $p < 0.001$) and the interaction between time and SS treatment ($p = 0.03$; Table 1). Treatment level comparisons showed that mussels in 0, 25, and 1250 mg L^{-1} had significantly greater mean SLs at the experiment end (Fig. 2A, Table S3). Mussels grew over time, and the greatest growth was in the highest, lowest, and control treatments.

Mussel attachment location at experiment end, expressed as the percent of mussels attached to mesh versus the tank bottom, ranged from 29 % in the 10 mg L^{-1} treatment to 87 % in 500 mg L^{-1} (mean = 63 %). Mussel attachment to suspended mesh was significantly related to SS concentration ($p < 0.001$; Fig. 3A, Table S4), with the lower concentrations (10, 25, 50, and 100 mg L^{-1}) negatively related to mesh settlement (Table S5). Mussels preferentially settled on the bottom of the tank in low concentration SS treatments.

3.2. Chronic SS exposure experiment

Mean mussel mortality was relatively low in all treatments (range = 1–30 %; mean = 12 %) and not affected by SS treatment ($p = 0.42$; Fig. 1B, Table S6).

Table 1

Type III ANOVA table summarising the results of linear mixed model to test the effect of 10 suspended sediment concentrations (SS Treatment) and time (experiment outset vs. end) on mussel shell length in short term experiment (5 days). * refers to model interaction.

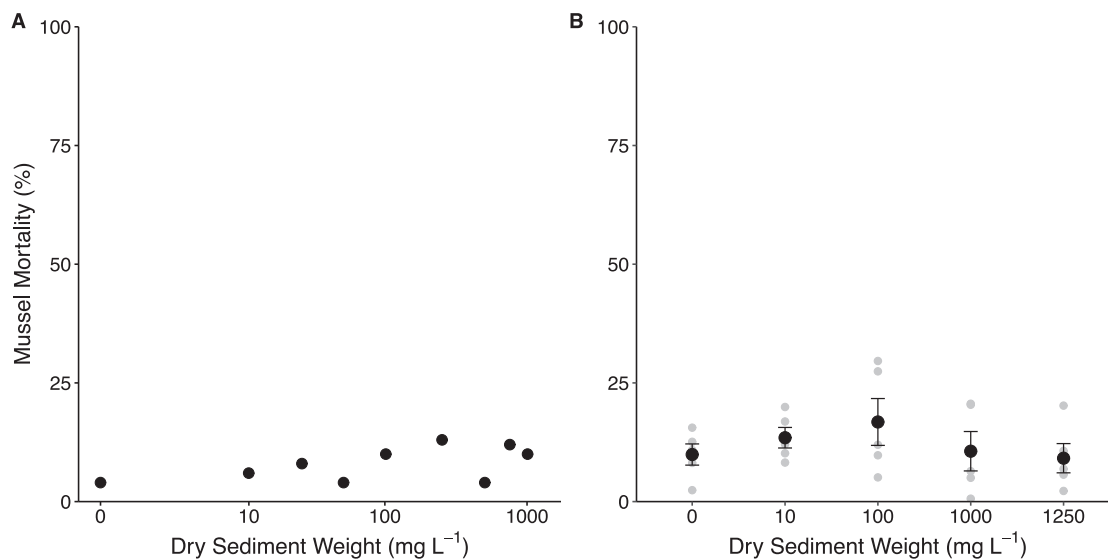| Model Parameter	SumSq	MeanSq	Df	F-Value	p-Value
SS Treatment	0.81	0.09	9, 2	0.30	0.92
Time	5.27	5.27	1, 924	17.34	<0.001
SS Treatment*Time	5.61	0.62	9, 924	2.054	0.03

Fig. 1. Percent of juvenile mussel spat (*Perna canaliculus*) that died following exposure to different levels of suspended sediment concentrations over (A) 5 day short term and (B) 30 day long term experiments. Grey dots in (B) are the mortality in each tank, and black dots are the mean (± SE) mortality per treatment level. There was no significant difference among treatments for either experiment (A or B).
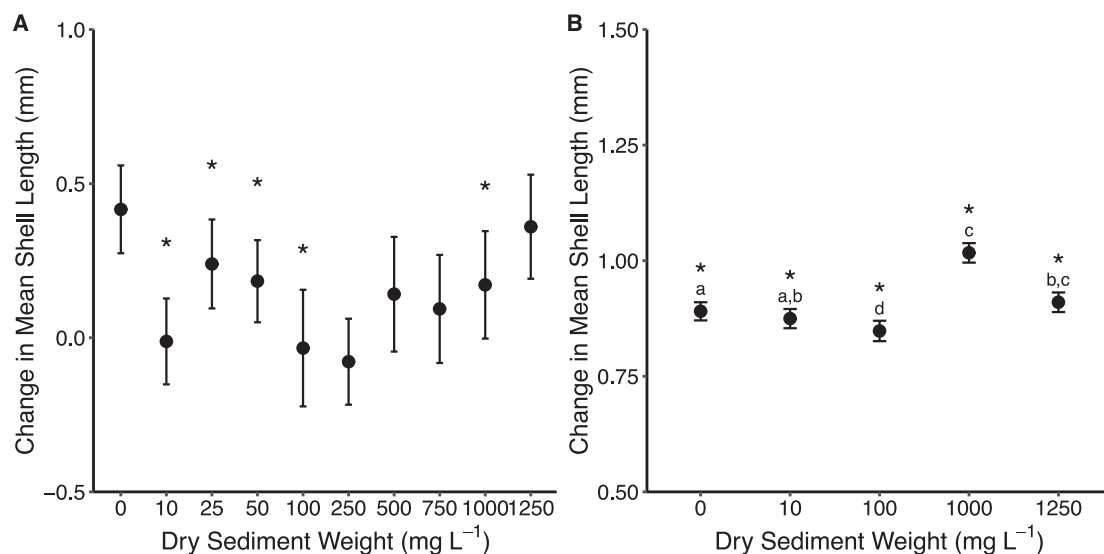
Fig. 2. Change in mean juvenile mussel (*Perna canaliculus*) shell length over time exposed to a range of suspended sediment treatments in (A) 5 day short term experiment and (B) 30 day long term experiment. * represents a significant change in length over experiment duration ($p < 0.001$ in both experiments, A and B). Different letters in (B) represent significant differences among treatments.
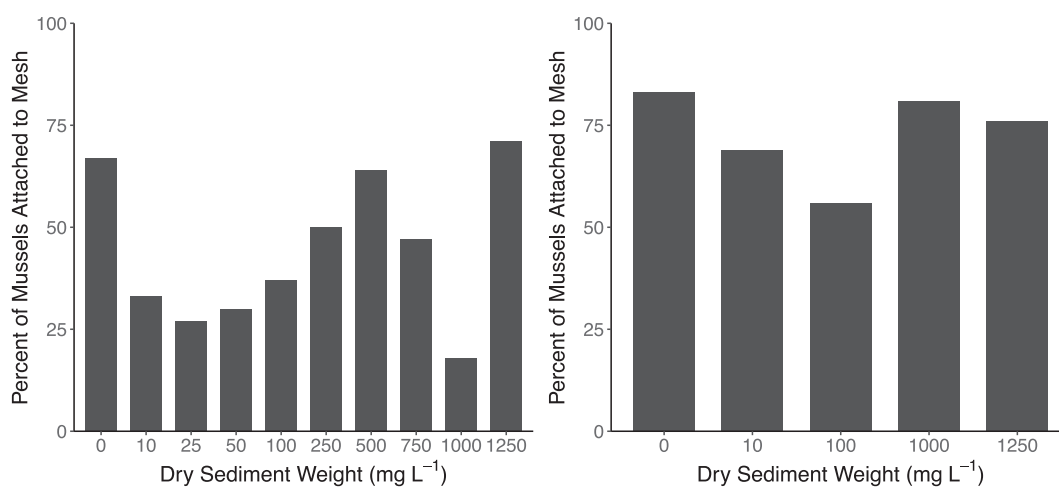

Fig. 3. Percent of juvenile mussels (*Perna canaliculus*) attached to mesh relative to tank bottom following (A) 5 day short term experiment and (B) 30 day long term experiment.

Mussel SLs at the experiment outset ranged from 0.31 to 2.71 mm (mean = 1.35 mm) and 0.61 to 6.55 mm (mean = 2.26 mm) at the end of the chronic exposure experiment. Mean mussel SL was related to both time (outset vs. end; $p < 0.001$) and the interaction between time and SS treatment ($p < 0.001$, Table 2). Post hoc contrasts showed that mean mussel SLs were significantly greater at experiment end than outset at all treatment levels ($p < 0.001$; Table S7) and that no treatment levels differed from each other at experiment outset. The two highest SS treatments (1000, 1250 mg L^{-1}) had significantly greater SLs at

Table 2
Type III ANOVA table summarising the results of linear mixed model testing effect of five suspended sediment concentrations (SS Treatment) and time (experiment outset vs. end) on mussel shell lengths in long term experiment (30 days). * refers to interaction term.

Model Parameter	SumSq	MeanSq	Df	F-Value	*p*-Value
SS Treatment	0.30	0.08	4, 20	0.196	0.94
Time	3052.14	3052.14	1, 29,248	7885.386	<0.001
SS Treatment*Time	13.46	3.37	4, 29,247	8.695	<0.001

experiment end than the other treatments (Fig. 2B, Table S8). The highest SS treatments caused the greatest mussel growth.

Mussel final attachment location, expressed as the percent attached to the mesh versus the tank bottom, ranged from 56 % in the 100 mg L^{-1} treatment to 83 % in the 0 mg L^{-1}. Mussel attachment to suspended mesh was significantly related to SS concentration ($p = 0.001$; Fig. 3B, Table S9), with the lower concentrations (10, 100 mg L^{-1}) negatively related to settlement on the mesh (Table S10). Settlement was significantly higher on the mesh than on the bottom at every treatment concentration except for 10 mg L^{-1} ($p < 0.001$; Table S11). Settlement location and its interaction with SS treatment increased mussel growth ($p < 0.001$, Table 3). Growth was higher on the mesh than the bottom and in the higher SS concentrations (relative to lower concentrations; Table S12).

The percent TOM of mussels was 17.8–37.6 % (mean = 26.0 %) at the end of the experiment (Fig. 4A). The calorific content of mussels at the end of the experiment ranged from 74.3 to 1770.0 cal g^{-1} of AFDW (Fig. 4B). There was no difference in mussel percent TOM ($p = 0.74$, Table S13) or mussel calorific content among SS treatments ($p = 0.27$,

Table 3

Type III ANOVA table summarising the results of linear mixed model on the effect of five different suspended sediment concentrations (SS Treatment) and mussel settlement location (Location) on mussel growth in long term experiment (30 days). * refers to interaction.

Model Parameter	SumSq	MeanSq	Df	F-Value	*p*-Value
SS Treatment	0.43	0.11	4, 20	0.26	0.90
Location	112.64	112.64	1, 21,022	278.69	<0.001
SS Treatment*Location	45.09	11.27	4, 21,022	27.89	<0.001

Table S14).

3.3. Sediment analyses

The percent TOM of the sediment was 8.0 ± 0.3 % before the experiment and 4.0 ± 2.0 % after. The grain size of the sediment primarily comprised medium and coarse silt (i.e., 15.6–31, 31–63 μm) grain sizes, with 22.8 % of the sample volume in each category. In the recovered sediment, the grain size distribution was centred on the coarse silt (31–63 μm) size with 51.7 % (Fig. 5).
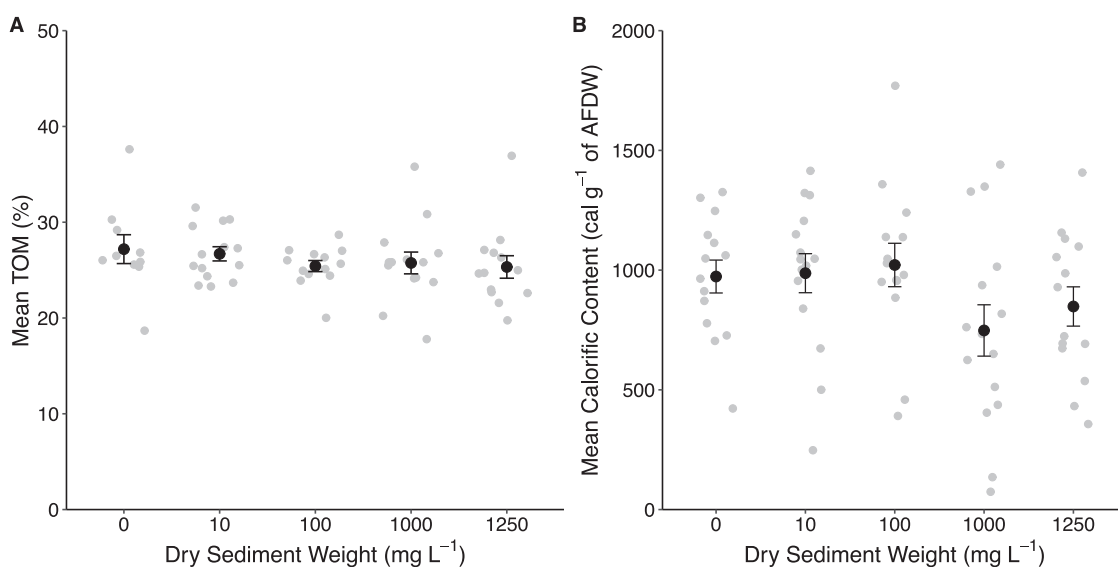

Fig. 4. (A) Mean percent total organic matter (TOM) and (B) calorific content of juvenile mussels (*Perna canaliculus*) exposed to suspended sediment (SS) over 30 day long term experiment. Grey dots show replicate measurements from experimental tanks, and black dots show mean (± SE) per SS treatment level. There was no significant difference among treatments for either measure. AFDW, ash-free dry weight.
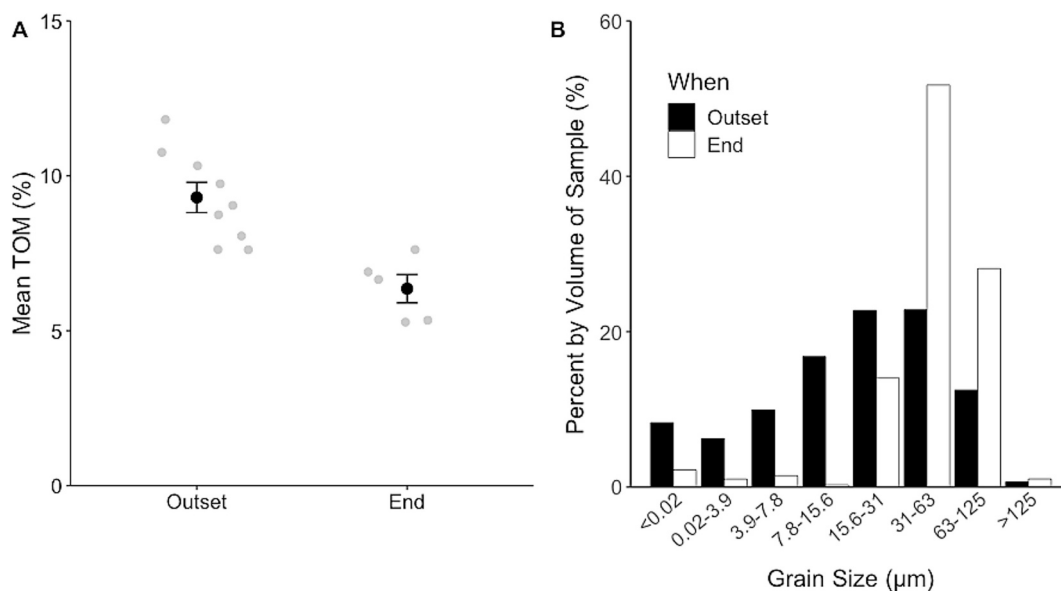

Fig. 5. Characteristics of the sediment used in experiments. (A) Mean percent total organic matter (TOM) of sediment (± SE) used in the suspended sediment treatments in the 30 day long term exposure experiment at the outset of the experiment and as recovered at the end (pooled treatments). Grey dots show replicate percent TOM samples and black dots are the mean per time period. (B) Grain size analysis of sediment.

4. Discussion

4.1. Mussel mortality

Small *P. canaliculus* (< 6 mm shell length (SL)) are prone to gill filament blockage and damage when exposed to suspended food particles >15 μm (Gui et al., 2016b). Hence, exposure to high concentrations of <63 μm suspended sediment could be expected to decrease survival due to gill damage and blockage. However, the overall mortality of mussel spat exposed to SS, even at extremely high SS (i.e., 1000), was relatively low and not different from spat in the treatment without sediment following the acute (5 day) experiment. This result could have been due to the short experimental duration. However, at the end of the chronic exposure experiment (30 day), the mean mortality of mussel spat was only slightly higher than after the acute exposure experiment, again with no difference detected among treatments. These results suggest that green-lipped mussel spat can survive at least 30 days in the high SS conditions tested in these experiments.

The highest SS concentration tested in the chronic exposure experiment (1250 mg L^{-1}) could be expected in highly human-disturbed watersheds (e.g., agriculture, construction) and/or following an extreme weather event (e.g., cyclone, flood, landslide) (Ellis et al., 2002; Yanai et al., 2006). However, these elevated SS levels do not typically last for $\geq$30 days in coastal oceans and estuaries. Particle settling times in the ocean are complex and challenging to predict, being influenced by many factors, including wind, waves, tides, and particle shape and size (Nasiha and Shanmugam, 2018; Osborne and Greenwood, 1993; Sutherland et al., 2015). However, particle settling is substantially increased in seawater vs. freshwater and high particle concentrations due to aggregates forming with increased density (Kranck, 1980; Lick et al., 1993; Sutherland et al., 2015). Hence, sediment particles typically settle through the mixed layer within days (Lande and Wood, 1987), and prolonged exposure to suspended sediment concentrations of this magnitude would likely require repeated mass sediment inputs, most likely the result of cumulative events. For example, in Fiji, following mass forest burning, a major rainstorm event triggered 620 landslides in the following weeks (Nunn, 1990). In New Zealand, Cyclone Bola (1988) triggered 184 landslides per km^2, and an extreme rainfall event in 2004 triggered thousands of landslides over 16,000 km^2 (Crozier, 2005). While the results of the current study may not extend to the extreme events listed here, they do suggest that green-lipped mussel spat survival is reasonably robust to suspended sediment.

4.2. Mussel shell growth

Mussel shell growth was positively correlated with the interaction between time and suspended sediment (SS) concentration at both time scales (5 and 30 days). This result is consistent with previous studies that have found increased bivalve growth with high levels of SS (Colden and Lipcius, 2015; Dekshenieks et al., 1993; Emerson, 1990) and, in particular, clay addition (Aucoin and Himmelman, 2011; Bricelj and Malouf, 1984; Gatenby et al., 1996; Soniat et al., 1984; Sornin et al., 1988). Juvenile *Elliptio complanata* (unionid mussel) and *Mercenaria mercenaria* (clam/quahog) both had increased growth in suspended sediments (Cyr, 2020; Davis, 1960; Dekshenieks et al., 1993), while *Limnoperna fortunei* (freshwater mussel) "D" larval stage size was positively correlated with the inorganic:organic matter ratio (Eilers et al., 2011). Additionally, *Mytilus edulis* fed pure algae alone were unable to reach the same growth rates achieved with silt-addition diets (Soniat et al., 1984).

Although sediment-mediated growth enhancement is well supported in the literature, there is little agreement over the mechanism that supports this growth. Theories include that the sediment provides a physical substratum for aiding with mechanical digestion, an enzymatic digestion enhancer, or a source of micronutrients (Gatenby et al., 1996; Urban and Langdon, 1984). For example, in diet experiments,

Placopecten magellanicus (Atlantic sea scallop) had very low absorption of organic matter from sediment but very high nitrogen absorption (Cranford and Grant, 1990). Additionally, sediment may aid in the retention of small food particles (Deslous-Paoli, 1985; Sornin et al., 1988) and play a role in pedal feeding in juvenile bivalves with underdeveloped feeding structures (Gatenby et al., 1996; Hua et al., 2013; Reid et al., 1992). While the mechanism behind this pattern of SS-enhanced growth may be specific to the species and their environment, its determination could aid in bivalve restoration and aquaculture work. For example, increased shell growth due to specific nutrients in the sediment could lead to the formulation of growth-enhancing dietary supplements.

4.3. Mussel nutritional condition

While sediment-aided growth is primarily regarded as being due to dietary supplementation through whatever mechanism, the increased growth could also be viewed as a strategy to limit vulnerability to environmental perturbation (Aucoin and Himmelman, 2011). The latter theory spurred the testing of mussel nutritional condition to determine whether the increased growth had measurable physiological costs. Prolonged exposure (30 days) to high SS concentrations (up to 1250 mg L^{-1}) was expected to negatively impact mussel condition due to the following: 1) higher energy expenditures and reduced feeding capacity from the physical demand and time spent filtering and sorting, and 2) loss of energy from mucous and psuedofaeces production. However, the percent TOM and calorific content of mussels showed no differences among treatments. Although not significant, there was a trend of lowered mean calorific content in the two highest SS treatments, suggesting that the food intake or energy expenditure of these mussels may have been marginally altered (Table S15). However, these results show that, under the conditions tested here, mussel spat can endure high SS (up to 1250 mg L^{-1} for 30 days) with no measurable cost to nutritional condition.

4.4. Mussel final attachment location

The attachment location of mussel spat at experiment end was significantly related to SS treatment in both experiments (5, 30 days), with more mussels settled on the tank bottom at low SS concentrations. Mussels have complex settlement behaviour, which may contain multiple settlement and drift stages (Bayne, 1964). This may explain the results observed here. If the conditions on the tank became unsuitable at higher concentrations (more turbid, burial risk), the mussels might have re-joined the water column to find a more favourable habitat. These results suggest that high SS triggers detachment and migration of mussel spat, which may be an important factor limiting recruitment in wild mussel populations exposed to episodic high SS events.

Wild and restored mussel beds in New Zealand have been limited by recruitment, with high sediment loads implicated as the cause. In this study, suspended sediment had no impact on mortality or nutritional condition and a positive effect on growth. However, despite the lack of evidence for sediment negatively impacting mussels, it still triggered them to detach and depart the tank bottom in high SS concentrations. Larval settlement is highly dependent on settlement cues and attachment substrates (Alfaro et al., 2006; Wilcox et al., 2020). Suspended sediment may, thus, disrupt settlement cues and cover settlement substrates, making them unfavourable for mussel settlement. This study provides strong support for the theory that suspended sediment interrupts mussel settlement and should be explored further in future research.

4.5. Sediment analyses

The percentage TOM of the stock sediment (8.0 ± 0.3 %) agrees with previous studies on mudflat sediments (Cai et al., 2013; Carneiro et al.,

2021; Cheng and Chang, 1999; Christie et al., 2000), showing that it was representative of what would likely be experienced in the natural environment. The percent TOM of the recovered sediment was lower than the start (4.0 ± 2.0 %), suggesting that some of the organic material was ingested and assimilated by the mussels or utilised through bacterial activity. Additionally, the mean grain size of the recovered sediment appears to have shifted towards larger grains, suggesting that fine grains were retained (e.g., clogging the gills) or aggregated by mucous during pseudofaeces production and were unrecovered during the sediment recovery process.

5. Conclusions

This study explored the survival, growth, and nutritional condition of mussel (*P. canaliculus*) spat under a range of suspended sediment (SS) concentrations at two time scales (5 and 30 days) to determine whether SS could be an explanatory factor in declining mussel populations and struggling restoration efforts. The results here provide strong evidence that mussel spat are relatively robust to high SS concentrations over time scales relevant to extreme weather events, with high survival and increased growth. However, high SS concentrations triggered detachment and departure, with mussels presumably attempting to escape unfavourable conditions. This result may explain the low recruitment numbers in mussel restoration and should be further explored in future research. Additionally, this study shows potentially advantageous effects of high SS levels on mussel growth, which may have restoration and aquaculture implications.

CRediT authorship contribution statement

Brandy S. Biggar: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Andrew Jeffs:** Writing – review & editing, Validation, Methodology, Funding acquisition, Conceptualization. **Jenny R. Hillman:** Writing – review & editing, Validation, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data and code are available on Mendeley doi: 10.17632/v74xmgcwgg.1, link: data.mendeley.com/datasets/v74xmgcwgg/1.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2024.152074.

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