

## RESEARCH ARTICLE OPEN ACCESS

# The Use of Suspended Substrate to Facilitate Juvenile Mussel Recruitment in Restored Mussel Reefs

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## ABSTRACT

Mussel reefs have been depleted globally by overfishing and habitat degradation, but the advent of reef restoration has produced promising results in terms of adult mussel survival and biodiversity enhancement. However, an absence of juvenile recruitment into restored mussel reefs is regularly cited as jeopardising their persistence and expansion. This lack of recruitment has been associated with concurrent loss of macroalgae which would provide for the settlement of larvae and facilitate the establishment of juvenile mussels. This research investigated whether the provision of filamentous material (coir rope) would enable the recruitment of green-lipped mussels (*Perna canaliculus*) among adult mussels on the seabed. The settlement of juveniles over the 4-month experimental period was low (i.e., 12.6–24.9 juveniles m<sup>-1</sup> coir) and was only observed on the coir and not in the adult mussel reefs or muddy seabed. Importantly, observed settlement on the coir did not lead to recruitment onto the seabed. Notably, all green-lipped mussel juveniles settled on the provided coir rope were small (345.4 ± 5.0 µm) and there was no change in size of settled juveniles over a 4-month period. Therefore, only primary settlers selected the coir rope and settled juveniles either migrated or died soon after settlement. This suggests that larval supply and post-settlement processes and survival are constraining recruitment to restored mussel reefs. Evaluating larval supply, optimising substrate positioning and greater understanding of post-settlement processes, such as secondary settlement behaviour and interference in settlement by sedimentation, can help to improve global mussel restoration methods.

## 1 | Introduction

Reef-forming bivalves, especially mussels and oysters, have been severely impacted by overharvesting and degradation of coastal environments throughout many parts of the world (Beck et al. 2011; Lotze et al. 2006). Additionally, other anthropogenic stressors including climate change have also played a role in the decline of many reef-forming bivalve populations from issues such as rising sea temperatures, air temperatures and increased predator pressure (Groscholz and Ruiz 1996; Jones et al. 2010; Steeves et al. 2018). Reef-forming bivalves provide a plethora of ecosystem services, such as biogenic habitat formation (Benjamin et al. 2022; Hancock and zu Ermgassen 2018; Ní

Mhurchú et al. 2026), sediment stabilisation (Meadows et al. 1998) and denitrification (Sea et al. 2021). Furthermore, many reef-forming bivalves hold significant cultural value (Reeder-Myers et al. 2022) and many wild populations are also economically important through harvesting or providing wild seed for aquaculture (Grabowski et al. 2012).

The importance of reef-forming bivalves and the lack of natural recovery of their populations have led to a growth of restoration interventions. However, the restoration of reef-forming bivalves faces diverse and complex challenges (Morgan and Rakocinski 2022; zu Ermgassen et al. 2020), especially the facilitation of juvenile recruitment (Arribas et al. 2015; Fitzsimons et al. 2020;

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Morgan and Rakocinski 2022). Recruitment success can be affected by factors such as larval supply, connectivity (Theuerkauf et al. 2021), nutrition (Lagarde et al. 2017; Phillips 2002), predation (Esquivel-Muelbert et al. 2022) and sedimentation (Biggar et al. 2025; Poirier et al. 2021). Habitat degradation has also been prominent among the reasons for the lack of recovery of bivalve reefs and often directly impacts recruitment processes (Beck et al. 2011; Lotze et al. 2006), especially through the damage and removal of attachment substrates, such as through seabed dredging when used as a method of harvesting benthic bivalves (Beck et al. 2011; Gillies et al. 2018; McAfee et al. 2024).

Numerous restoration efforts for reef-forming bivalves have focused on the provision of additional substrate to facilitate recruitment (Bersoza Hernández et al. 2018; Fitzsimons et al. 2020), especially in oyster restoration (Harding et al. 2012; Lipcius and Burke 2018; Schulte et al. 2009). There are some species-specific settlement preferences for oysters that are based on the rugosity and material composition of substrates, but competent larvae will generally settle and establish onto most rigid surfaces if the environmental conditions are suitable (Holliday et al. 1993; Perog et al. 2023; Tamburri et al. 2008). In contrast to oysters, many mussel species demonstrate a preference for settling and attaching to more flexible and filamentous substrates such as macroalgae or conspecific byssus threads (Alfaro 2006b; de Nesnera 2016; van der Heide et al. 2014). This process where larval mussels metamorphose from a planktonic stage, settle and attach to a substrate as early juveniles (i.e., plantigrades) is termed primary settlement (Bayne 1964). Juvenile mussels have markedly more complex settlement processes than oysters given their ability to readily sever their byssus threads and relocate, enabling them to settle and attach to different substrates throughout their juvenile development, a process termed secondary settlement, before eventually recruitment is achieved where juveniles become established within adult mussel reefs (Bayne 1964; Le Corre et al. 2013; Newell et al. 2010).

Due to primary and secondary settlement requirements, restoration of mussels in substrate-limited environments may also require the restoration of beneficial macroalgae (Toone et al. 2024). However, co-restoration using macroalgae adds complexity to bivalve restoration with additional husbandry, logistic and biosecurity challenges (Wood et al. 2024). Therefore, the provision of alternative settlement substrates may be a more efficient method to alleviate substrate limitation. For example, research on blue mussels (*Mytilus edulis*) in the Netherlands, restored mussel reefs by threading coir (a filamentous coconut fibre rope) through mesh as an alternative settlement substrate to address the lack of available macroalgae that the species naturally settles on (Temminck et al. 2021). Identifying the critical bottleneck of substrate availability in conjunction with understanding species substrate preferences allows methods to be developed to effectively address this important component of recruitment for restoration purposes (Temminck et al. 2021).

The historical overharvesting and habitat degradation for wild populations of green-lipped mussels, *Perna canaliculus*, in Aotearoa – New Zealand, typifies the plight of reef-forming bivalves across the globe (Thurstan et al. 2024; Toone et al. 2023a; Zu Ermgassen et al. 2012). Extensive subtidal and intertidal populations of green-lipped mussels were decimated, largely

by dredge and hand-gathering fisheries throughout the 1900s, with little to no recovery in these populations observed in subsequent decades (Paul 2012; Toone et al. 2023a). This lack of recovery has prompted efforts to restore historical mussel reefs through transplanting adults sourced from aquaculture; however, despite large numbers of spawning adult mussels present in close proximity on long-line aquaculture farms, the persistence of these reefs is limited due to a lack of juvenile recruitment (Benjamin, Jeffs, et al. 2023; Toone et al. 2023b; Wilcox et al. 2018). The importance of substrate structure and complexity for the settlement of green-lipped mussel juveniles has been well described (Burnham et al. 2025; Jeffs et al. 2018; Wu, Anderson, et al. 2025). For example, there is an inverse relationship between juvenile green-lipped mussel size and the degree of branching in the settlement substrate with primary settlers most commonly recorded on more filamentous macroalgae and hydroids, whilst larger juveniles are more commonly found attached to coarser branching substrate (Alfaro and Jeffs 2002).

Concurrently with the depletion of green-lipped mussel populations in Aotearoa – New Zealand, dredging and benthic habitat degradation have decimated the coverage of co-occurring macroalgae in some locations, including the filamentous macroalgae that can play an important role in juvenile mussel recruitment (Ulrich and Handley 2020). The loss of macroalgae from locations which historically hosted wild mussel reefs could be causing substrate limitation for larval settlement and establishment of early juveniles, creating a critical roadblock in the mussel life cycle and impeding natural recovery of these important reef-forming mussels (Toone et al. 2023c; Ulrich and Handley 2020). For example, the provision of macroalgae successfully facilitated the settlement of mussels in an experiment comparing translocated macroalgae species in Kenepuru Sound (Toone et al. 2023d), and installing macroalgae was shown to increase the recruitment of blue mussels (*Mytilus* spp.) to the nearby rocky seabed (Toone et al. 2024). Alternative substrates have also proved effective in achieving juvenile green-lipped mussel settlement and recruitment. For example, biodegradable ropes were fabricated from native plant species in Ōhiwa Harbour, Aotearoa – New Zealand, and were used to successfully facilitate the recruitment of green-lipped mussels in pilot-scale restoration research (Paul-Burke, Ngarimu-Cameron, Burke, et al. 2022). Coir could provide similar outcomes and is the primary settlement substrate used in Aotearoa – New Zealand's only commercial green-lipped mussel hatchery (South et al. 2017). Using coir for restoration could allow for the deployment of large quantities of settlement substrate while avoiding production bottlenecks of native plant-based ropes and the difficulties associated with the harvest and husbandry of large quantities of live macroalgae.

This study aimed to test whether providing filamentous substrate (i.e., coir rope) for primary settlement can facilitate recruitment of green-lipped mussels into adult mussels directly below the substrate. Furthermore, this experiment aimed to determine if adult mussels provide effective substrate for settlement of juvenile green-lipped mussels in soft-sediment subtidal environments for which recruitment research has been limited. Determining whether a lack of settlement substrate is constraining recruitment into green-lipped mussel reefs will help inform future restoration efforts for both this mussel species and other mussel species of similar habit globally.

## 2 | Methods

### 2.1 | Location Description

This experiment was conducted in Skiddaw (41° 11' 55.5" S 173° 54' 52.0" E) in Kenepuru Sound, within the Marlborough Sounds at the north-eastern tip of the South Island of Aotearoa – New Zealand (Nicol 2011). Historically, populations of green-lipped mussels were present in Skiddaw (Stead 1971), but, prior to recent restoration efforts, only scattered individuals remained in the low intertidal (Toone et al. 2023a). The study site has nine restored subtidal plots (each plot approximately 9 m<sup>2</sup> in size) at a depth of 5–7 m containing adult green-lipped mussels sourced from aquaculture and transplanted onto the seabed in January 2020 (Benjamin, Handley, et al. 2023). The mussels established successfully, but no juvenile recruitment was observed by the end of monitoring in January 2022 (Benjamin, Handley, et al. 2023).

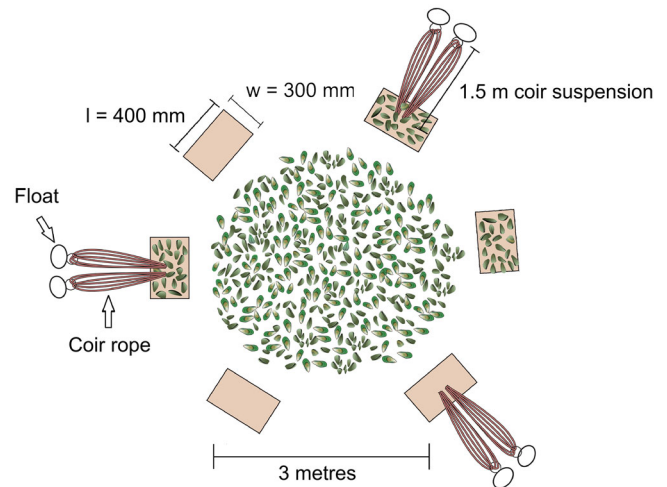
### 2.2 | Experimental Design

Small black plastic trays (400 × 300 × 130 mm) with a 2.3 kg concrete weight attached to the underside of the tray were used to isolate discrete areas of seabed that could be easily removed for sampling. Six randomly selected restored mussel plots each had six trays deployed within 0.3 m of the perimeter by SCUBA divers between 6 and 13 February 2024, with a total of 36 trays deployed. Trays were deployed at this time because February–April is the peak season for green-lipped mussel larval settlement based on aquaculture industry monitoring at this location for over 20 years (Atalah and Forrest 2019). All trays were filled with a 30–60 mm layer of mud covering the base of the tray that was collected from the adjacent seabed. To determine the localised influence of adult mussel presence on juvenile settlement and recruitment, half of the trays (18) were randomly selected and each had 20 adult mussels (70–130 mm shell length) sourced from a local mussel farm (supplied by Sanford Ltd.), transplanted on top of the mud within the trays. Nine randomly selected trays with mud and adult mussels and nine with mud only, each had two 15 m bundles of coir rope attached to the base of the trays using zip ties and suspended in the water column 1.5 m above the trays using net floats (Figure 1).

Overall, this resulted in four treatments ( $n = 9$  trays each); (1) Mussels with coir, (2) Mussels only, (3) Coir only and (4) Bare sediment.

### 2.3 | Sampling

Three replicate trays from each of the four treatments were randomly selected from the six plots for sampling at three times after deployment, 2 weeks (27 February 2024), 6 weeks (26 March 2024) and 16 weeks post-deployment (6 June 2024). For the collection of the trays, SCUBA divers removed the coir from the tray and placed it into a plastic ziplock bag underwater. Each tray was then enclosed in a cotton sack with a mesh size of <10 µm to contain any juvenile mussels present. The sacks were then attached by rope to surface floats for recovery from the surface.



**FIGURE 1** | Schematic of experimental trays containing mud and four different treatments (i.e., Mussels with coir, Mussels only, Coir only and Bare sediment) randomly positioned around six sub-tidal plots of restored adult mussels (only one plot pictured in schematic). Sampling occurred 2, 6 and 26 weeks post-deployment. Mussel treatments each contained 20 adult mussels per tray, and coir treatments had suspended bundled coir attached.

At the surface, adult mussels were removed from the trays, assessed for survival based on their ability to close their valves and then bagged. The mud in all trays was collected, and the sides of trays were scraped to recover any attached juveniles. Coir, adult mussels and mud from within the trays were each frozen separately to allow for later processing.

### 2.4 | Processing

After freezing (−20 °C), each substrate type (coir, adult mussels and mud) for each replicate was independently washed with pressurised freshwater to detach any juveniles (Himiona et al. 2026b; Jeffs et al. 2018; Toone et al. 2023c) and collected over three screen sizes to make counting more efficient (1000, 500 and 180 µm mesh screen). Material retained on the 1000 and 500 µm screens were examined under a microscope for green-lipped mussels and blue mussels; however, no mussels at these size grades were observed. The contents of each sample on the 180 µm screen included large quantities of sediment, and effective counting required sub-sampling by homogenising in 1 L of freshwater and then collecting six random 5 mL sub-samples for examination. All green-lipped mussels and blue mussels in sub-samples were counted. For each replicate, 10 green-lipped mussels and 10 blue mussels were measured from the 5 mL sub-samples using a gridded petri dish to randomly select the mussels. Selected mussels were photographed and measured along the anterior–posterior axis (shell length) in ImageJ (Schneider et al. 2012). Blue mussels were included in this study as they are regularly observed establishing among green-lipped mussels on mussel farms, with settlement of blue mussels increasing in recent years (Forrest and Atalah 2017; McDougall et al. 2022). Two species of blue mussels are present in Kenepuru Sound, the native *Mytilus aoteanus* (although this species is not currently recognised by the World Register of Marine Species;

WorRMS Editorial Board 2026) and the invasive *Mytilus galloprovincialis* (Ravalo 2024). Due to difficulty in distinguishing the two blue mussel species at early life stages without genetic techniques, they were not distinguished in these counts and were reported as *Mytilus* spp.

## 2.5 | Industry Sampling

The Marine Farming Association in Aotearoa – New Zealand conducts a monitoring programme for the settlement of green-lipped and blue mussels which includes a sampling site at Skiddaw (Atalah and Forrest 2019; Toone et al. 2022), adjacent to the experimental location (approximately 600 m away where the water depth is 13–15 m), the data from which were used for comparison with counts obtained from this experiment. This sampling programme uses frames containing a standardised single 25 cm length of polypropylene filamentous rope of the type used for commercial spat catching deployed at two depths, 2 and 10 m, deployed from mussel farms. During the study period, the sampling ropes were deployed for 1 week at the beginning of each month from December 2023–May 2024. Following each 1 week deployment, the numbers of recently settled juvenile green-lipped and blue mussels on the ropes were counted. The counts were plotted for visual assessment over this period, which was concurrent with the experiment.

## 2.6 | Statistical Analyses

No settlement was observed in the sediment or on adult mussels for any treatments; therefore, counts of juvenile green-lipped mussels recovered from only the coir were compared, and for consistency with other research on juvenile mussel counts (Atalah and Forrest 2019; Toone et al. 2022), means for juvenile counts from subsamples were scaled to the total 1 L concentrated sample volume and divided by the 30 m rope length to determine juveniles  $m^{-1}$  of rope. Juvenile counts were analysed using a generalised linear mixed-effects model (GLMM) with a negative binomial distribution to account for overdispersed count data observed in testing. Treatment and sampling event were included as fixed effects along with their interaction. Tray identity was included as a random effect to account for non-independence among repeated subsamples for counts from the same replicate. Inclusion of plot as an additional random effect was evaluated but explained negligible variance and did not improve model fit; therefore, the final model retained tray identity as the only random effect. Where significant effects were detected, pairwise comparisons of estimated marginal means were performed using Tukey-adjusted  $p$ -values. Predicted means are presented as estimated marginal means derived from the fitted GLMMs rather than raw means as estimated marginal means account for the experimental design, random tray effects and the non-Gaussian error structure of the data, ensuring consistency between reported values and statistical inference. All statistical analyses were conducted in R, 4.4.0 (R Core Team 2026). The glmmTMB package (McGillucuddy et al. 2025) was used for mixed-effects modelling and emmeans (Lenth 2023) for extracting marginal means and pairwise contrasts. DHARMA (Hartig 2016) was used for all model diagnostics (dispersion,

zero-inflation and Kolmogorov–Smirnov test of residual uniformity).

As for green-lipped mussels, no settlement of blue mussels was observed in the sediment or on adult mussels for any treatments; therefore, counts of juvenile blue mussels recovered from only the coir were compared. No settlement of blue mussels was observed at weeks 2 and 6, therefore a different approach for statistical analyses was required. For week 16, where blue mussels were present, the counts of blue mussels were compared between treatments using a two-sample Welch's  $t$ -test based on replicate-level data ( $n = 3$  per treatment). A Wilcoxon rank-sum test was also performed to account for potential deviations from normality.

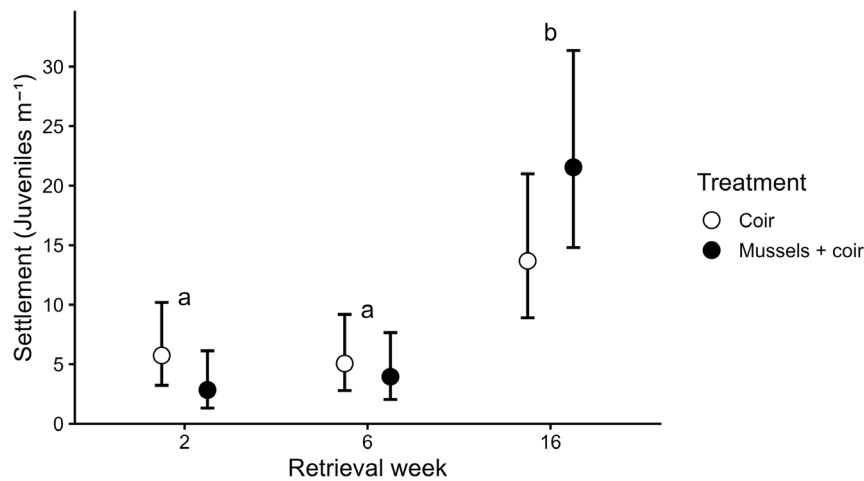
The shell lengths of juvenile green-lipped mussels were analysed using a linear mixed-effects model to account for the hierarchical structure of the sampling design. Treatment and sampling week were included as fixed effects along with their interaction. The replicate was included as a random effect, nested within treatment and week, to account for non-independence among mussels sampled on the same rope replicate. Individual mussel shell lengths were used as the response variable, and the significance of fixed effects was assessed using Type III ANOVA with Satterthwaite's approximation of degrees of freedom. The lmerTest package was used for modelling green-lipped mussel size data (Kuznetsova et al. 2017). For the sampling at week 16 where blue mussels were present, the mean shell length of juvenile blue mussels per replicate was calculated and compared between treatments using a two-sample  $t$ -test. Replicates were treated as the unit of replication to avoid pseudoreplication arising from multiple measurements within each replicate.

Adult survival was analysed using a binomial generalised linear model with a logit link, with survival specified as the number of individuals alive out of the 20 transplanted per tray. The model included treatment, sampling week and their interaction as fixed effects. Overdispersion was detected and accounted for using a quasibinomial error structure, and significance was assessed using analysis of deviance with  $F$ -tests. Due to small sample size and complete separation at the final time point, treatment differences at each week were also assessed using Fisher's exact tests. Estimated marginal means were used to obtain predicted survival probabilities on the response scale.

## 3 | Results

### 3.1 | Green-Lipped Mussel Settlement

Coir was the only substrate where juvenile green-lipped mussels were present, with no juvenile green-lipped mussels found on either mud or adult mussels in any of the trays. There were significantly more juveniles (i.e., more than double) settled at week 16 than at both weeks 2 and 6 (Figure 2;  $p < 0.05$ ). At week 16, there was no difference in the mean number of juvenile green-lipped mussels on the coir rope between the two treatments, Mussels with coir and Coir alone treatments (Table S1; Figure 2). However, there was a significant treatment and time



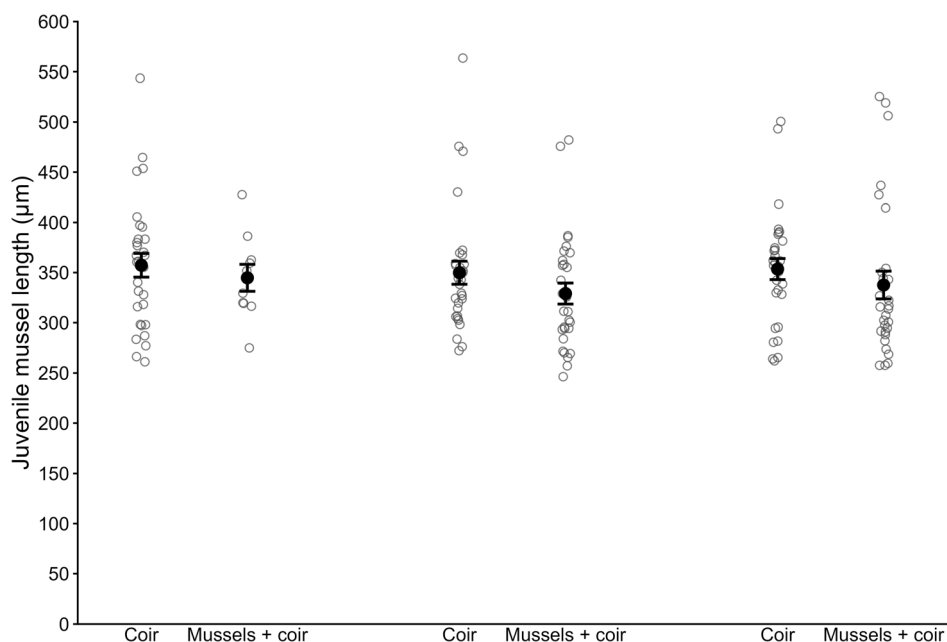
**FIGURE 2** | Mean settlement (juveniles  $m^{-1} \pm 95\%$  confidence intervals) of juvenile green-lipped mussels on sampled coir for two treatments (i.e., Coir and Mussels with coir) for three sampling events (2, 6 and 16 weeks;  $n = 3$  for each treatment and sampling event). Mean settlement was derived from estimated marginal means from a negative binomial GLMM. Different letters above sampling weeks indicate statistically significant differences among sampling events based on estimated marginal means averaged across treatments ( $p < 0.05$ ). No significant differences were detected between treatments within any sampling event.

interaction (Table S1), indicating that patterns of settlement differed between treatments through time despite no significant treatment differences being detected within individual retrievals (Table S2; Figure 2).

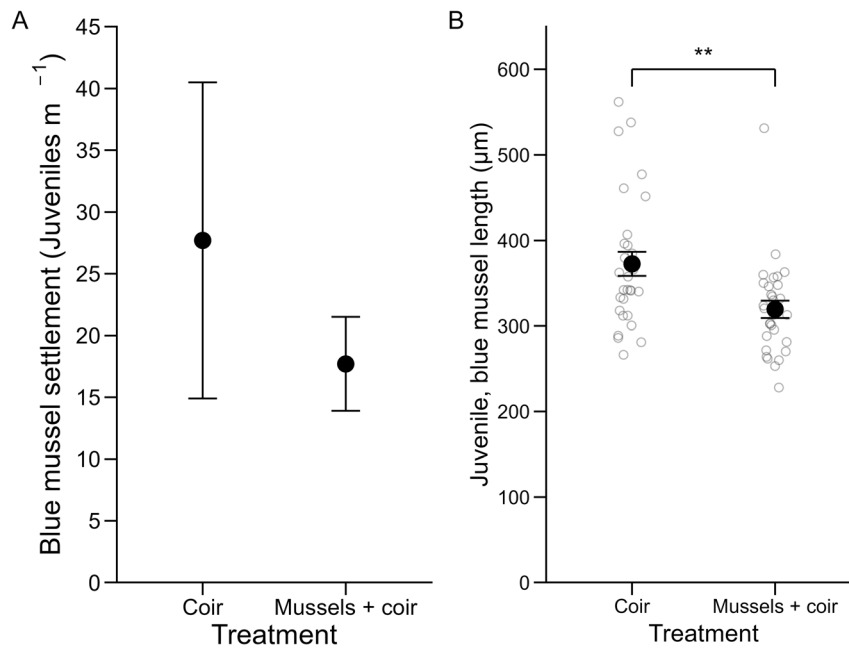
The overall mean shell length  $\pm$  SE of settled green-lipped mussels on coir rope was  $345.4 \pm 5.0 \mu m$  (Figure 3). There was no significant effect of treatment or sampling event on the mean shell length of juvenile green-lipped mussels, and no significant interaction between these factors was observed (Tables S3 and S4).

### 3.2 | Blue Mussel Settlement

Coir was also the only substrate where juvenile blue mussels were present, with no settlement of blue mussels observed at weeks 2 or 6. Therefore, only counts for week 16 could be analysed. Within week 16, there was no significant effect of treatment ( $t = 0.75$ ,  $p = 0.52$ ) on the number of settled blue mussel juveniles (Figure 4). There was a significant effect of treatment on blue mussel shell length ( $t = 7.92$ ,  $p = 0.014$ ) with the mean shell length of blue mussels on the Coir treatment larger ( $p = 0.014$ ) than those on the Mussels with coir treatment.



**FIGURE 3** | Mean shell length of juvenile green-lipped mussels settled on coir rope in two treatments (i.e., Coir and Mussels with coir) for three sampling events (2, 6 and 16 weeks). Small open circles indicate individual recorded shell lengths, and large filled circles indicate mean shell lengths of three replicates for each treatment and sampling event except for Mussels with coir in week 2 where mussel settlement only occurred on one replicate. Error bars indicate standard errors.



**FIGURE 4** | Mean blue mussel settlement (juveniles m<sup>-1</sup>) (A) and shell length (μm) (B) settled on coir rope in two treatments, (i.e., Coir and Mussels with coir) at 16 weeks post deployment. Large, filled points indicate treatment means with standard errors, and small open circles in (B) indicate individual recorded shell lengths of the three replicates per treatment. Mean juvenile shell length was significantly smaller in the Mussels with coir treatment compared to the Coir treatment ( $p = 0.014$ ). Error bars indicate standard errors.

### 3.3 | Adult Mussels

All mussels remained within their respective trays throughout the experiment, whether alive or dead, as indicated by the presence of their shells. At all sampling events, there was no significant difference in adult mussel survival for treatment ( $p = 0.41$ ), sampling event ( $p = 0.10$ ) or their interaction ( $p = 0.88$ ; Table 1). Fisher's exact tests also detected no significant differences at individual sampling events (all  $p = 1.00$ ), but, notably, overdispersion and complete separation at week 16 were observed.

### 3.4 | Industry Monitoring of Settlement

Counts for green-lipped mussel settlement made by the Marine Farming Association during the months of March–May at the Skiddaw site coinciding with the experimental deployment peaked in February (the week before trays were deployed) and an overall mean  $\pm$  SE of  $172.9 \pm 48.1$  juveniles m<sup>-1</sup> over both depths and for all months (Figure 5). Overall, industry counts for blue mussel settlement had a mean  $\pm$  SE of  $868.2 \pm 431.4$  juveniles m<sup>-1</sup> and varied month by month with a peak in June.

**TABLE 1** | Mean adult green-lipped mussel survival (%  $\pm$  standard error) for 20 mussels within benthic trays at three sampling events.

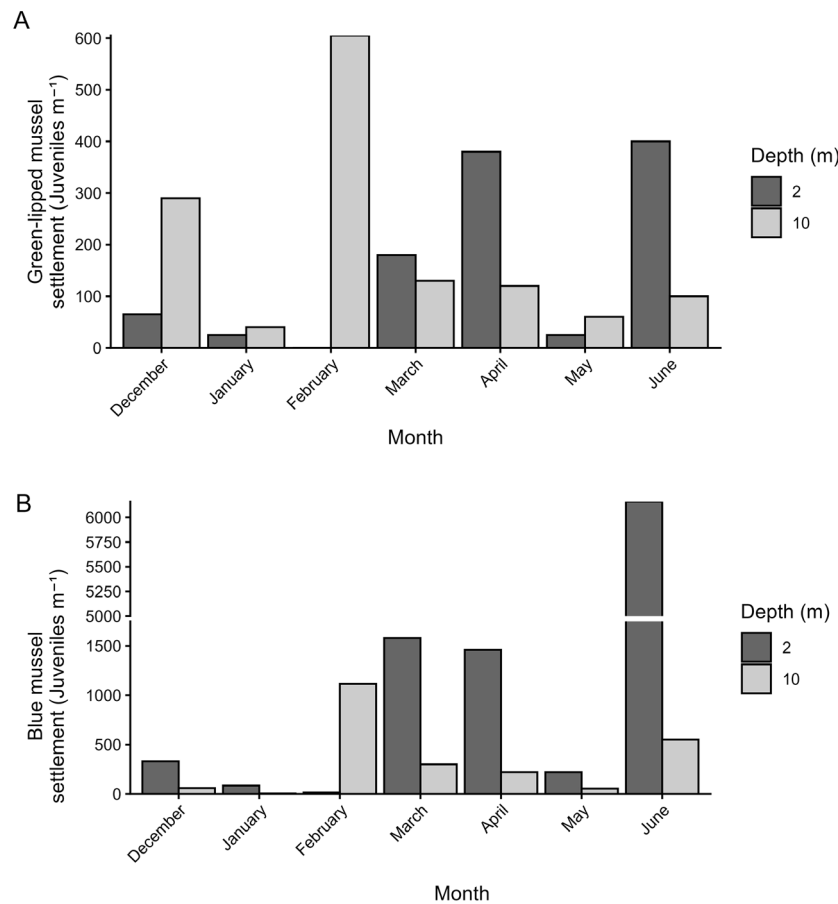
|         | Mussels           | Mussels with coir |
|---------|-------------------|-------------------|
| Week 2  | 95.0% $\pm$ 2.9%  | 83.3% $\pm$ 10.1% |
| Week 6  | 81.7% $\pm$ 10.1% | 46.7% $\pm$ 25.2% |
| Week 16 | 0.0% $\pm$ 0.0%   | 77% $\pm$ 13.6%   |

## 4 | Discussion

Recruitment of juvenile bivalves is a commonly cited barrier to achieving self-sustaining populations, which frustrate efforts to restore degraded bivalve reefs in many parts of the world (Arribas et al. 2015; Fitzsimons et al. 2020; Morgan and Rakocinski 2022). This study identifies important patterns in settlement of juvenile green-lipped mussels that can help guide future efforts to conserve and restore mussel populations. Importantly, settlement of juvenile green-lipped and blue mussels was exclusively observed on the coir rope, consistent with studies that identify flexible, filamentous substrates as an effective primary settlement substrate for mussels (Alfaro and Jeffs 2002; Jeffs et al. 2018; Temmink et al. 2021). Therefore, ensuring the presence of filamentous substrate within the proximity of mussel reefs may be critical for facilitating primary settlement, and this natural recruitment pathway appears to have been lost through the decline of filamentous seaweed in the surrounding natural benthic habitat (Toone et al. 2023a).

### 4.1 | Ontogenetic Differences

In this study, only recently settled larvae were observed on the coir, with no increase in juvenile shell length over successive sampling events for green-lipped mussels. Green-lipped mussels typically undergo primary settlement at a shell length of 250–300 μm (Redfearn et al. 1986), and the mean shell length of settled mussels encountered in this study was  $345.4 \pm 5.0$  μm, indicating that settled mussels were recent primary settlers. Primary settlers were likely to have regularly migrated in search of more suitable habitat, resulting in their continual replacement by newly settled larvae. Within aquaculture, losses of seeded,



**FIGURE 5** | Monthly settlement of juvenile green-lipped mussels (juveniles m<sup>-1</sup>) (A) and blue mussels (juveniles m<sup>-1</sup>) (B) at two depths (2 and 10 m) as measured by sampling conducted by the Marine Farming Association from December 2023 to June 2024. Bars represent counts of settled juvenile mussels at each depth for each sampling month. Due to a peak in blue mussel settlement in June, a break in the y-axis between 2000 and 5000 juveniles m<sup>-1</sup> is used in panel B.

green-lipped mussel juveniles on polypropylene commercial ropes are commonly higher than 80% (Skelton et al. 2024; South et al. 2020) while turnover of migrating and settling juvenile mussels is known to change as frequently as daily (South 2016). Therefore, secondary settlement behaviour likely played a role in the consistent juvenile size observed throughout the 4-month experimental period.

Despite evidence of primary settlement on the coir substrate, this did not translate into successful recruitment of juvenile green-lipped or blue mussels to the seabed directly beneath the substrate during the 4-month study period. Juvenile green-lipped mussels readily crawl from biodegrading substrate such as coir to nearby substrates (South et al. 2017). This behaviour is routinely utilised in the aquaculture industry where juvenile green-lipped mussels initially settle on coir as a primary settlement substrate before transferring to polypropylene rope of a greater surface area for attachment (South et al. 2017). However, because the coir in this experiment was suspended up to 1.5 m above the seabed, advection likely occurred, with juvenile mussels detaching from the substrate and being transported horizontally before re-settling on secondary substrates, as is observed in numerous mussel species (Commuto et al. 2014; Newell et al. 2010; Wu, Lundquist, et al. 2025). Furthermore, the mucous drifting behaviour that is commonly

expressed by green-lipped mussels for secondary migration is highly effective at facilitating dispersal (i.e., juveniles dispersed a mean net distance of 3–8 km in one study; Wu, Lundquist, et al. 2025). Consequently, the absence of juvenile green-lipped mussels among the adult mussels positioned directly below the coir may reflect longer-range secondary migration, rather than pedal crawling down or dropping from the coir ropes to underlying adult mussels. Recruitment may have been facilitated by the coir into the adjacent restored reefs or other substrates beyond the immediate experimental area. Such recruitment would not have been detected by the sampling design, which focused on the area immediately below the substrate, and detection may have been limited by the small scale of this experiment. Furthermore, restored green-lipped mussel reefs currently occur at a much smaller spatial scale than the extensive seafloor habitats they historically occupied (Toone et al. 2023a), which may reduce the likelihood of migrating juveniles successfully locating and settling onto suitable reef habitat.

Although secondary settlement behaviour is well documented in juvenile green-lipped mussels, the mechanisms that initiate this behaviour remain poorly understood (Skelton et al. 2021). While small juvenile green-lipped mussels appear to undertake secondary migratory behaviour more readily (Ram et al. 2026), it is also possible that conditions, such as high juvenile density, substrate

degradation and low turbulence or oxygen, may trigger the initiation of secondary migration soon after larvae have settled on coir (Himiona et al. 2025; Sanjayasari and Jeffs 2019; South et al. 2020). The presence of various substrates, each with different characteristics, on remnant mussel reefs has been correlated with different ontogenetic stages of green-lipped mussel juveniles (Burnham et al. 2025). This suggests that a variety of substrates may be needed to accommodate secondary settlement beyond the initial primary settlement substrate. Notably, hatchery-reared juvenile green-lipped mussels are settled on coir rope, but the coir is wrapped around coarser polypropylene ropes for deployment in coastal waters in an effort to increase retention of the mobile juveniles by allowing them to readily relocate to the coarser rope that has greater surface area (South et al. 2017). Coir rope alone may not offer such a diverse range of settlement substrates that would otherwise attract and retain secondary settlers. A better understanding of the process of secondary migration, especially the triggers for this behaviour and patterns of juvenile migration, will likely result in improved restoration interventions and outcomes.

Importantly, the absence of growth among settled juveniles may not have been solely the result of secondary migration. Mortality or reduced growth caused by environmental constraints could also have contributed to the observed pattern. A multitude of environmental stressors can impact growth and survival of juvenile bivalves following larval settlement, such as hydrodynamics, temperature and salinity (Fuentes-Santos and Labarta 2015; Himes et al. 2024; Miller et al. 2017). Green-lipped mussel fitness is also likely to be adversely affected by climate change through exposure to stressors such as marine heatwaves and increasingly frequent harmful algal blooms (Delorme et al. 2020; Greenhough et al. 2025). Primary settlement is a particularly sensitive stage in the bivalve life cycle. Successful development can be influenced by stressors through larval stages such as nutrition (Lagarde et al. 2017; Toupoint et al. 2012), periods of starvation during larval stages (Phillips 2002) or toxicity of land-derived metals (McDougall et al. 2022; Vignier et al. 2025). These results highlight that primary settlement substrate represents only one component of the complex recruitment process and that additional components in the settlement–recruitment pathway need to be addressed to effectively facilitate recruitment for green-lipped mussel restoration.

## 4.2 | Larval Supply

Understanding the thresholds of larval supply required for successful recruitment events is important for guiding future conservation and restoration efforts for green-lipped mussels. For example, research on blue mussels (*Mytilus* spp.) indicates that recruitment is episodic and requires peaks of exceptionally high larval input to achieve meaningful recruitment (Le Corre et al. 2013). The quantities of settled, juvenile green-lipped mussels in this study were low in contrast with those observed previously in several other mussel settlement studies within this study area and elsewhere in Aotearoa – New Zealand, where counts have regularly been in the thousands per metre (Forrest and Atalah 2017; Himiona et al. 2026a; Toone et al. 2022). The low settlement observed may simply be a result of substantial spatial and temporal (both inter- and intra-annual) variability in settlement of

green-lipped mussels that has been observed in the Marlborough Sounds (Atalah and Forrest 2019). Similarly, low settlement was observed in a 2023 study attempting to use macroalgae to facilitate recruitment of green-lipped mussels also in Kenepuru Sound (Toone et al. 2024), although settlement onto experimental macroalgae was substantially higher in a study in the previous year (Toone et al. 2023c). Furthermore, aquaculture industry monitoring that occurs within 600 m of the study site demonstrated that peak settlement for the 2023–2024 season was observed the week prior to the deployment of this experiment, with a count of 605 juveniles  $m^{-1}$ . Therefore, the deployment timing of this experiment may have either missed a specific settlement event, as they vary widely or there may have been lower overall availability of settling larvae during the study year. Alternatively, aquaculture industry monitoring over the last 40 years has demonstrated a downward trend of settlement rates for green-lipped mussels during 2010–2020 despite large quantities of farmed mussels now regularly spawning and presumably contributing to the larval pool (McDougall et al. 2022). Determining if larval supply is constraining recruitment for green-lipped mussel restoration is critical and potentially shapes the methodology for restoration in other bivalve species (Grizzle et al. 2021; Pogoda et al. 2020; zu Ermgassen et al. 2020).

## 4.3 | Optimising Substrate Positioning

The positioning of the substrate in the water column could have further influenced the low rates of juvenile green-lipped and blue mussel settlement observed in this current study. Experimental substrate provision for oyster restoration indicates that depth, relief of substrate from the seabed and water column position all influence larval settlement and juvenile recruitment (Baillie and Grabowski 2019; Poirier et al. 2019; Saavedra et al. 2024). Importantly, settlement behaviour differs between bivalve species. For example, a study identified that Pacific oysters (*Magallana gigas*) settled mostly at the bottom of the water column, while Mediterranean mussels settled on substrates in the middle of the water column (Audrézet et al. 2022). Settlement of mussels was higher (predominantly of *Mytilus* spp.) on substrate that was deployed closer to the sea-surface compared to identical substrate deployed at the seabed in Kenepuru Sound (Toone et al. 2024). Optimising the position of settlement substrate in the water column to maximise the settlement of target mussel species could be critical given the interspecific differences in mussel settlement behaviour. Although settlement of blue mussel juveniles in this study was similarly low compared to green-lipped mussels, aquaculture industry counts from June 2024 recorded 6160 juveniles  $m^{-1}$  at 2 m depth, which was 10-fold higher than settlement at 10 m depth. Therefore, optimising deployment depth of settlement substrate could reduce competition from blue mussels during the settlement of green-lipped mussels.

The proximity of substrate to the seabed may also be an important contributor to settlement of green-lipped mussel larvae because sediment resuspension is likely to affect the substrate closest to the seabed (Yang et al. 2016). In the present study, coir substrate was suspended only 1.5 m above the seabed and, upon recovery, all the substrates were fouled with sediment regardless of depth. Sedimentation has increased markedly in the last

60 years at the study site (Urlich and Handley 2020) with an increasing frequency of severe weather events exacerbating this further (Swales et al. 2021). Elevated suspended sediment may affect juvenile green-lipped mussels by disrupting feeding, inhibiting settlement and increasing the risk of post-settlement burial (Biggar et al. 2026; Gui et al. 2016; Poirier et al. 2021). Evidently, processes such as larval behaviour, interspecific competition and sedimentation may interact with depth and proximity to the seabed to influence juvenile green-lipped mussel settlement and recruitment. However, these relationships remain poorly understood and require further research to inform recruitment facilitation.

#### 4.4 | Adult Conspecific Effects

Previous research has identified positive relationships between juvenile green-lipped mussels and adult green-lipped mussels. For example, studies have recorded higher densities of primary settling juveniles on settlement materials deployed within restored mussel reefs in comparison with control areas (Benjamin, Handley, et al. 2023; Wilcox et al. 2020). In the current study, all treatments were near the restored mussel reef; however, the treatment with adult mussels directly below the coir substrate did not increase the primary settlement or retention of settled green-lipped mussel juveniles on coir. Additionally, there was no settlement of juvenile green-lipped or blue mussels onto adult mussels in the trays. The absence of primary settlement onto adult mussels in this study may reflect environmental stressors such as sedimentation, limiting benthic settlement. However, it may indicate that adult mussels are not a preferred primary settlement substrate, which is consistent with the absence of reports of primary settlement onto adult mussels in the existing literature. Adult conspecific presence could be detrimental for primary settlement, with cannibalism significantly affecting primary settlement in species such as the Mediterranean mussel (Porri et al. 2008) and cannibalism of larvae has been recorded in green-lipped mussels (Alfaro 2006a). Crucially, green-lipped mussel juveniles larger than 1 mm in shell length have been recorded attached to adults in studies on remnant green-lipped mussel reefs (Burnham et al. 2025), in restoration (Toone et al. 2023c) and in the laboratory (Wilcox and Jeffs 2017). Understanding the relationship between adult conspecifics and recruitment of juvenile green-lipped mussels is important in a restoration context as most current methods rely on transplanting adult mussels to restoration sites (Benjamin, Jeffs, et al. 2023; Toone et al. 2023b). Inducing settlement is complex in bivalves and unlikely to be solely reliant on adult conspecific presence with other environmental influences on settlement including biofilms and chemical and microbial cues (Ganesan et al. 2012; Morello and Yund 2016; Rato et al. 2025). Determining the minimum size at which juvenile green-lipped mussels will select to settle among adult conspecifics as well as identifying other factors driving this migration will better inform intermediary steps required to optimise restoration and facilitate transfer from primary settlement to within green-lipped mussel reefs.

A lack of juvenile green-lipped mussel recruitment may also have been impacted by similar stressors that could have caused the variation observed in adult mussel survival. Low survival of

transplanted bivalves is common (Overton et al. 2024) and numerous stressors are known to limit adult survival, such as population density and temperature (Ericson et al. 2023; Overton et al. 2024). Predation is another potential cause of adult mortality (Overton et al. 2024) and researchers have observed widespread predation of adult green-lipped mussels by sea stars (Paul-Burke, Ngarimu-Cameron, Paul, et al. 2022; Wilcox and Jeffs 2019), including correlations with survival of restored reefs in the same area as this study (Benjamin et al. 2022; Benjamin, Jeffs, et al. 2023). Although data was not collected on predators in this study, numerous sea stars within trays and on the restored reefs were observed by divers during sample collections. Furthermore, predation is a major cause of mortality for juvenile bivalves worldwide. For example, blue crabs (*Callinectes sapidus*) prey on eastern oyster recruits (Lin et al. 2024), while sea stars are important predators of juvenile blue mussels in the Dutch Wadden Sea (Zhao et al. 2024). In the Gulf of Maine, USA, populations of blue mussels have been severely reduced by the invasive green crab (*Carcinus maenas*), whose expansion and increasing abundance have been facilitated by climate change (Commuto et al. 2019). Additionally, chemical cues from predators can deter settlement of bivalves and reduce settlement induction effects of adult conspecifics (Morello and Yund 2016; Pruett and Weissburg 2019; Schmidlin et al. 2024). Consequently, the cause of adult mortality recorded in this study could also have caused reduced numbers of juveniles on the coir or among adult mussels due to direct predation or reduced settlement due to deterrence cues.

#### 5 | Conclusion

This study demonstrates that the provision of filamentous substrate is important for facilitating primary settlement of mussels. However, increased settlement did not translate into recruitment of juvenile mussels to adult mussel reefs directly below the substrate. The scarcity of larger green-lipped and blue mussel juveniles observed on the provided coir substrate, together with their complete absence among adult mussels, highlights the need to understand and facilitate intermediary processes linking primary settlement to recruitment. Improved understanding is required of the triggers for secondary settlement, patterns of dispersal (i.e., short vs. long range dispersal), the ontogenetic stage at which juveniles will settle among adult mussels and the influence of adult mussel reef size on recruitment success. Furthermore, the low densities and small size of settling juvenile green-lipped mussels observed in this study may reflect natural spatial and temporal variability in settlement patterns. Alternatively, they may indicate recruitment bottlenecks that warrant further research, including limitations of larval quantity, reduced larval quality and low post-settlement survival. Such constraints could be driven by habitat degradation including sedimentation, reduced food quality and heavy metal contamination. Further opportunities to optimise restoration methods include research on substrate positioning, which is likely to be influenced by larval behaviour, hydrodynamic conditions and interspecific competition. A more comprehensive understanding of the processes that influence recruitment throughout the mussel life-cycle will support the development of increasingly

targeted restoration methods capable of promoting self-sustaining mussel reef populations.

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## Ethics Statement

No ethical approval was required for this study.

## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The datasets generated during and/or analysed during the current study are available in the The University of Auckland data repository at [10.17608/k6.auckland.32934917](https://doi.org/10.17608/k6.auckland.32934917).

## References

- Alfaro, A., and A. Jeffs. 2002. "Small-Scale Mussel Settlement Patterns Within Morphologically Distinct Substrata at Ninety Mile Beach, Northern New Zealand." *Malacologia* 44: 1–15.
- Alfaro, A. C. 2006a. "Evidence of Cannibalism and Benthic-Pelagic Coupling Within the Life Cycle of the Mussel, *Perna canaliculus*." *Journal of Experimental Marine Biology and Ecology* 329, no. 2: 206–217. <https://doi.org/10.1016/j.jembe.2005.09.002>.
- Alfaro, A. C. 2006b. "Population Dynamics of the Green-Lipped Mussel, *Perna canaliculus*, at Various Spatial and Temporal Scales in Northern New Zealand." *Journal of Experimental Marine Biology and Ecology* 334, no. 2: 294–315. <https://doi.org/10.1016/j.jembe.2006.02.004>.
- Arribas, L. P., M. Bagur, J. L. Gutiérrez, and M. G. Palomo. 2015. "Matching Spatial Scales of Variation in Mussel Recruitment and Adult Densities Across Southwestern Atlantic Rocky Shores." *Journal of Sea Research* 95: 16–21. <https://doi.org/10.1016/j.seares.2014.10.015>.
- Atalah, J., and B. M. Forrest. 2019. "Forecasting Mussel Settlement Using Historical Data and Boosted Regression Trees." *Aquaculture Environment Interactions* 11: 625–638. <https://doi.org/10.3354/AEI00337>.
- Audrézet, F., A. Zaiko, P. Cahill, et al. 2022. "Does Plastic Type Matter? Insights Into Non-Indigenous Marine Larvae Recruitment Under Controlled Conditions." *PeerJ* 10: e14549. <https://doi.org/10.7717/peerj.14549>.
- Baillie, C. J., and J. H. Grabowski. 2019. "Factors Affecting Recruitment, Growth and Survival of the Eastern Oyster *Crassostrea virginica* Across an Intertidal Elevation Gradient in Southern New England." *Marine Ecology Progress Series* 609: 119–132. <https://doi.org/10.3354/meps12830>.
- Bayne, B. 1964. "Primary and Secondary Settlement in *Mytilus edulis* L. (Mollusca)." *Journal of Animal Ecology* 33, no. 3: 513–523. <https://doi.org/10.2307/2569>.
- Beck, M. W., R. D. Brumbaugh, L. Airoidi, et al. 2011. "Oyster Reefs at Risk and Recommendations for Conservation, Restoration, and Management." *BioScience* 61, no. 2: 107–116. <https://doi.org/10.1525/bio.2011.61.2.5>.
- Benjamin, E. D., S. J. Handley, R. Hale, T. A. Toone, A. Jeffs, and J. R. Hillman. 2022. "Biodiversity Associated With Restored Small-Scale Mussel Habitats Has Restoration Decision Implications." *Biodiversity and Conservation* 31, no. 11: 2833–2855. <https://doi.org/10.1007/s10531-022-02462-1>.
- Benjamin, E. D., S. J. Handley, A. Jeffs, L. Olsen, T. A. Toone, and J. R. Hillman. 2023. "Testing Habitat Suitability for Shellfish Restoration With Small-Scale Pilot Experiments." *Conservation Science and Practice* 5, no. 2: e12878. <https://doi.org/10.1111/csp2.12878>.
- Benjamin, E. D., A. Jeffs, S. J. Handley, T. A. Toone, and J. R. Hillman. 2023. "Determining Restoration Potential by Transplanting Mussels of Different Size Classes Over a Range of Aerial Exposures." *Marine Ecology Progress Series* 713: 71–81. <https://doi.org/10.3354/meps14337>.
- Bersoza Hernández, A., R. D. Brumbaugh, P. Frederick, et al. 2018. "Restoring the Eastern Oyster: How much Progress Has Been Made in 53 Years?." *Frontiers in Ecology and the Environment* 16, no. 8: 463–471. <https://doi.org/10.1002/fee.1935>.
- Biggar, B. S., A. Jeffs, and J. R. Hillman. 2025. "Effects of Suspended Sediment on Survival, Growth, and Nutritional Condition of Green-Lipped Mussel Spat (*Perna canaliculus*, Gmelin, 1791)." *Journal of Experimental Marine Biology and Ecology* 582: 152074. <https://doi.org/10.1016/j.jembe.2024.152074>.
- Biggar, B. S., A. Jeffs, and J. R. Hillman. 2026. "The Effects of Sudden Sediment Burial on Juvenile Green-Lipped Mussels." *Marine Biology* 173, no. 4: 61. <https://doi.org/10.1007/s00227-026-04818-5>.
- Burnham, K. A., J. R. Hillman, and A. G. Jeffs. 2025. "Macroalgae and Conspecifics Serve as Critical Attachment Substrates for Juvenile Green-Lipped Mussels (*Perna canaliculus*) During Different Stages of Development." *Journal of Experimental Marine Biology and Ecology* 588: 152108. <https://doi.org/10.1016/j.jembe.2025.152108>.
- Commito, J. A., A. E. Commito, R. V. Platt, et al. 2014. "Recruitment Facilitation and Spatial Pattern Formation in Soft-Bottom Mussel Beds." *Ecosphere* 5, no. 12: 1–26. <https://doi.org/10.1890/ES14-00200.1>.
- Commito, J. A., B. R. Jones, M. A. Jones, S. E. Winders, and S. Como. 2019. "After the Fall: Legacy Effects of Biogenic Structure on Wind-Generated Ecosystem Processes Following Mussel Bed Collapse." *Diversity* 11, no. 1: 11. <https://doi.org/10.3390/d11010011>.
- de Nesnera, K. L. 2016. "Stress, Ontogeny, and Movement Determine the Relative Importance of Facilitation for Juvenile Mussels." *Ecology* 97, no. 9: 2199–2205. <https://doi.org/10.1002/ecy.1505>.

- Delorme, N. J., L. Biessy, P. M. South, L. N. Zamora, N. L. C. Ragg, and D. J. Burritt. 2020. "Stress-on-Stress Responses of a Marine Mussel, *Perna canaliculus*: Food Limitation Reduces the Ability to Cope With Heat Stress in Juveniles." *Marine Ecology Progress Series* 644: 105–117. <https://doi.org/10.3354/meps13375>.
- Ericson, J., L. Venter, J. Copedo, V. Nguyen, A. Alfaro, and N. Ragg. 2023. "Chronic Heat Stress as a Predisposing Factor in Summer Mortality of Mussels, *Perna canaliculus*." *Aquaculture* 564: 738986. <https://doi.org/10.1016/j.aquaculture.2022.738986>.
- Esquivel-Muelbert, J. R., B. S. Lanham, F. Martínez-Baena, K. A. Dafforn, P. E. Gribben, and M. J. Bishop. 2022. "Spatial Variation in the Biotic and Abiotic Filters of Oyster Recruitment: Implications for Restoration." *Journal of Applied Ecology* 59, no. 4: 953–964. <https://doi.org/10.1111/1365-2664.14107>.
- Fitzsimons, J. A., S. Branigan, C. L. Gillies, et al. 2020. "Restoring Shellfish Reefs: Global Guidelines for Practitioners and Scientists." *Conservation Science and Practice* 2, no. 6: e198. <https://doi.org/10.1111/csp2.198>.
- Forrest, B. M., and J. Atalah. 2017. "Significant Impact From Blue Mussel *Mytilus Galloprovincialis* Biofouling on Aquaculture Production of Green-Lipped Mussels in New Zealand." *Aquaculture Environment Interactions* 9: 115–126.
- Fuentes-Santos, I., and U. Labarta. 2015. "Spatial Patterns of Larval Settlement and Early Post-Settlement Survivorship of *Mytilus galloprovincialis* in a Galician Ria (NW Spain). Effect on Recruitment Success." *Regional Studies in Marine Science* 2: 1–10. <https://doi.org/10.1016/j.rsma.2015.08.006>.
- Ganesan, A. M., A. C. Alfaro, C. M. Higgins, M. Duxbury, and J. D. Brooks. 2012. "Characterization of Biofilm Exudates and Their Effects on Settlement of Mussel (*Perna canaliculus*) Larvae." *Journal of Experimental Marine Biology and Ecology* 434: 34–46. <https://doi.org/10.1016/j.jembe.2012.07.026>.
- Gillies, C. L., I. M. McLeod, H. K. Alleyway, et al. 2018. "Australian Shellfish Ecosystems: Past Distribution, Current Status and Future Direction." *PLoS One* 13, no. 2: e0190914. <https://doi.org/10.1371/journal.pone.0190914>.
- Grabowski, J. H., R. D. Brumbaugh, R. F. Conrad, et al. 2012. "Economic Valuation of Ecosystem Services provided by Oyster Reefs." *BioScience* 62, no. 10: 900–909. <https://doi.org/10.1525/bio.2012.62.10.10>.
- Greenhough, H., K. F. Smith, J. Vignier, et al. 2025. "Impacts of Marine Heatwave Stress and Harmful Algal (*Alexandrium* spp.) Exposure on Subadult Green-Lipped Mussels (*Perna canaliculus*)." *Ecotoxicology and Environmental Safety* 304: 119112. <https://doi.org/10.1016/j.ecoenv.2025.119112>.
- Grizzle, R., K. Ward, R. Konisky, J. Greene, H. Abeels, and R. Atwood. 2021. "Oyster Reef Restoration in New Hampshire, USA: Lessons Learned During Two Decades of Practice." *Ecological Restoration* 39, no. 4: 260–273. <https://doi.org/10.3368/er.39.4.260>.
- Grosholz, E. D., and G. M. Ruiz. 1996. "Predicting the Impact of Introduced Marine Species: Lessons From the Multiple Invasions of the European Green Crab *Carcinus maenas*." *Biological Conservation* 78, no. 1-2: 59–66. [https://doi.org/10.1016/0006-3207\(94\)00018-2](https://doi.org/10.1016/0006-3207(94)00018-2).
- Gui, Y., L. N. Zamora, B. Dunphy, and A. G. Jeffs. 2016. "Understanding the Ontogenetic Changes in Particle Processing of the Greenshell Mussel, *Perna canaliculus*, in Order to Improve Hatchery Feeding Practices." *Aquaculture* 452: 120–127. <https://doi.org/10.1016/j.aquaculture.2015.07.035>.
- Hancock, B., and P. zu Ermgassen. 2018. "Enhanced Production of Finfish and Large Crustaceans by Bivalve Reefs." In *Goods and Services of Marine Bivalves*, 295–312. Springer International Publishing Cham.
- Harding, J. M., M. J. Southworth, R. Mann, and J. A. Wesson. 2012. "Comparison of, *Crassostrea virginica*, Gmelin (eastern Oyster) Recruitment on Constructed Reefs and Adjacent Natural Oyster Bars Over Decadal Time Scales." *Northeastern Naturalist* 19, no. 4: 627–646. <https://doi.org/10.1656/045.019.0407>.
- Hartig, F. 2016. *DHARMA: Residual Diagnostics for Hierarchical (multi-Level/Mixed) Regression Models*. CRAN: Contributed Packages.
- Himes, A. R., A. Schatz, and E. B. Rivest. 2024. "Differences in Larval Acidification Tolerance Among Populations of the Eastern Oyster, *Crassostrea virginica*." *Journal of Experimental Marine Biology and Ecology* 577: 152023. <https://doi.org/10.1016/j.jembe.2024.152023>.
- Himiona, K., A. G. Jeffs, and B. M. Skelton. 2025. "Exposure of Greenshell Mussel Spat (*Perna canaliculus*) to Stressors for Producing Single-Spat From Collector Ropes." *Aquaculture, Fish and Fisheries* 5, no. 4: e70097. <https://doi.org/10.1002/aff2.v5.4>.
- Himiona, K., A. G. Jeffs, and B. M. Skelton. 2026a. "Determining the Environmental Drivers of Greenshell Mussel (*Perna canaliculus*) Spat Settlement." *Aquaculture, Fish and Fisheries* 6, no. 2: e70219. <https://doi.org/10.1002/aff2.v6.2>.
- Himiona, K., A. G. Jeffs, and B. M. Skelton. 2026b. "Refining Spat-Collection Practices to Optimise Single-Seed Spat Production for New Zealand's Greenshell (*Perna canaliculus*) Mussel Industry." *Aquaculture, Fish and Fisheries* 6, no. 2: e70163. <https://doi.org/10.1002/aff2.v6.2>.
- Holliday, J. E., G. L. Allan, J. Frances, and L. P. Diver. 1993. "Evaluation of Commercially-Used Collectors for Sydney Rock Oysters, *Saccostrea commercialis* and Pacific Oysters, *Crassostrea gigas*." *Aquacultural Engineering* 12, no. 2: 63–79. [https://doi.org/10.1016/0144-8609\(93\)90017-6](https://doi.org/10.1016/0144-8609(93)90017-6).
- Jeffs, A. G., N. J. Delorme, J. Stanley, L. N. Zamora, and C. Sim-Smith. 2018. "Composition of Beachcast Material Containing Green-Lipped Mussel (*Perna canaliculus*) Seed Harvested for Aquaculture in New Zealand." *Aquaculture* 488: 30–38. <https://doi.org/10.1016/j.aquaculture.2018.01.024>.
- Jones, S. J., F. P. Lima, and D. S. Wetthey. 2010. "Rising Environmental Temperatures and Biogeography: Poleward Range Contraction of the Blue Mussel, *Mytilus edulis*, L., in the Western Atlantic." *Journal of Biogeography* 37, no. 12: 2243–2259. <https://doi.org/10.1111/jbi.2010.37.issue-12>.
- Kuznetsova, A., P. B. Brockhoff, and R. H. Christensen. 2017. "lmerTest Package: Tests in Linear Mixed Effects Models." *Journal of Statistical Software* 82: 1–26. <https://doi.org/10.18637/jss.v082.i13>.
- Lagarde, F., M. Ubertini, S. Mortreux, et al. 2017. "Recruitment of the Pacific Oyster *Crassostrea gigas* in a Shellfish-Exploited Mediterranean Lagoon: Discovery, Driving Factors and a Favorable Environmental Window." *Marine Ecology Progress Series* 578: 1–17. <https://doi.org/10.3354/meps12265>.
- Le Corre, N., A. L. Martel, F. Guichard, and L. E. Johnson. 2013. "Variation in Recruitment: Differentiating the Roles of Primary and Secondary Settlement of Blue Mussels *Mytilus* spp." *Marine Ecology Progress Series* 481: 133–146. <https://doi.org/10.3354/meps10216>.
- Lenth, R. V. 2023. *Emmeans: Estimated Marginal Means, Aka Least-Squares Means*. R Package version 1.10.2.
- Lin, C., B. A. Belgrad, C. M. Russell, J. Lunt, and D. L. Smee. 2024. "Phenotypic Plasticity Expands Oyster Survival and Realized Niche Space Across Tidal Elevations." *Marine Ecology Progress Series* 734: 35–43. <https://doi.org/10.3354/meps14561>.
- Lipcius, R. N., and R. P. Burke. 2018. "Successful Recruitment, Survival and Long-Term Persistence of Eastern Oyster and Hooked Mussel on a Subtidal, Artificial Restoration Reef System in Chesapeake Bay." *PLoS One* 13, no. 10: e0204329. <https://doi.org/10.1371/journal.pone.0204329>.

- Lotze, H. K., H. S. Lenihan, B. J. Bourque, et al. 2006. "Depletion, Degradation, and Recovery Potential of Estuaries and Coastal Seas." *Science* 312, no. 5781: 1806–1809. <https://doi.org/10.1126/science.1128035>.
- McAfee, D., L. D. McLeod, S. Carruthers, and S. D. Connell. 2024. "Reversing Functional Extinction: Successful Restoration of Eradicated Oyster Reefs." *Restoration Ecology* 32, no. 5: e14169. <https://doi.org/10.1111/rec.14169>.
- McDougall, D. R., T. A. Toone, and A. G. Jeffs. 2022. "Natural Heavy Metal Concentrations in Seawater as a Possible cause of Low Survival of Larval Mussels." *Journal of Trace Elements in Medicine and Biology* 74: 127071. <https://doi.org/10.1016/j.jtemb.2022.127071>.
- McGillcuddy, M., G. Popovic, B. M. Bolker, and D. I. Warton. 2025. "Parsimoniously Fitting Large Multivariate Random Effects in glmmTMB." *Journal of Statistical Software* 112: 1–19. <https://doi.org/10.18637/jss.v112.i01>.
- Meadows, P. S., A. Meadows, F. J. West, P. S. Shand, and M. A. Shaikh. 1998. "Mussels and Mussel Beds (*Mytilus edulis*) as Stabilizers of Sedimentary Environments in the Intertidal Zone." *Geological Society, London, Special Publications* 139, no. 1: 331–347. <https://doi.org/10.1144/GSL.SP.1998.139.01.26>.
- Miller, L. S., J. La Peyre, and M. La Peyre. 2017. "Suitability of Oyster Restoration Sites Along the Louisiana Coast: Examining Site and Stock x Site Interaction." *Journal of Shellfish Research* 36, no. 2: 341–351. <https://doi.org/10.2983/035.036.0206>.
- Morello, S. L., and P. O. Yund. 2016. "Response of Competent Blue Mussel (*Mytilus edulis*) Larvae to Positive and Negative Settlement Cues." *Journal of Experimental Marine Biology and Ecology* 480: 8–16. <https://doi.org/10.1016/j.jembe.2016.03.019>.
- Morgan, L. M., and C. F. Rakocinski. 2022. "Predominant Factors Limiting the Recovery of the Eastern Oyster (*Crassostrea virginica*) in Western Mississippi Sound, USA." *Estuarine Coastal and Shelf Science* 264: 107652. <https://doi.org/10.1016/j.ecss.2021.107652>.
- Newell, C. R., F. Short, H. Hoven, L. Healey, V. Panchang, and G. Cheng. 2010. "The Dispersal Dynamics of Juvenile Plantigrade Mussels (*Mytilus edulis* L.) From Eelgrass (*Zostera marina*) Meadows in Maine, USA." *Journal of Experimental Marine Biology and Ecology* 394, no. 1-2: 45–52.
- Ni Mhurchú, A., L. Johnston, J. R. Hillman, A. Jeffs, and E. D. Benjamin. 2026. "From Shell to Shelter: Investigating Small Reef Fish Abundance on Degraded Seafloor Restored With Mussels and Shell Material." *Restoration Ecology* 34: e70440. <https://doi.org/10.1111/rec.70440>.
- Nicol, A. 2011. "Landscape History of the Marlborough Sounds, New Zealand." *New Zealand Journal of Geology and Geophysics* 54, no. 2: 195–208.
- Overton, K., T. Dempster, S. E. Swearer, R. L. Morris, and L. T. Barrett. 2024. "Predictors of Outplanted Marine Bivalve Survival in Restoration: A Review and Synthesis." *Journal of Applied Ecology* 61, no. 12: 2884–2896. <https://doi.org/10.1111/1365-2664.14795>.
- Paul-Burke, K., R. Ngarimu-Cameron, J. Burke, et al. 2022. "Taura Kuku: Prioritising Māori Knowledge and Resources to Create Biodegradable Mussel Spat Settlement Lines for Shellfish Restoration in Ōhiwa Harbour." *New Zealand Journal of Marine and Freshwater Research* 56, no. 3: 570–584.
- Paul-Burke, K., R. Ngarimu-Cameron, W. Paul, et al. 2022. "Nga Tohu o Te Taiao: Observing Signs of the Natural World to Identify Seastar Over-Abundance as a Detriment to Shellfish Survival in Ōhiwa Harbour, Aotearoa/New Zealand." *New Zealand Sociology* 37, no. 1: 186–210.
- Paul, L. 2012. *A History of the Firth of Thames Dredge Fishery for Mussels: Use and Abuse of a Coastal Resource*. Ministry of Agriculture and Forestry.
- Perog, B. D., C. Bowers-Doerning, C. Y. L. Ramirez, et al. 2023. "Shell Cover, Rugosity, and Tidal Elevation Impact Native and Non-Indigenous Oyster Recruitment: Implications for Reef Ball Design." *Ecological Engineering* 192: 106969. <https://doi.org/10.1016/j.ecoleng.2023.106969>.
- Phillips, N. E. 2002. "Effects of Nutrition-Mediated Larval Condition on Juvenile Performance in a Marine Mussel." *Ecology* 83, no. 9: 2562–2574. <https://doi.org/10.2307/3071815>.
- Pogoda, B., P. Boudry, C. Bromley, et al. 2020. "NORA Moving Forward: Developing an Oyster Restoration Network in Europe to Support the Berlin Oyster Recommendation." *Aquatic Conservation: Marine and Freshwater Ecosystems* 30, no. 11: 2031–2037. <https://doi.org/10.1002/aqc.3447>.
- Poirier, L. A., J. C. Clements, M. R. Coffin, et al. 2021. "Siltation Negatively Affects Settlement and Gaping Behaviour in Eastern Oysters." *Marine Environmental Research* 170: 105432. <https://doi.org/10.1016/j.marenvres.2021.105432>.
- Poirier, L. A., J. C. Clements, J. D. P. Davidson, G. Miron, J. Davidson, and L. A. Comeau. 2019. "Sink Before You Settle: Settlement Behaviour of Eastern Oyster (*Crassostrea virginica*) Larvae on Artificial Spat Collectors and Natural Substrate." *Aquaculture Reports* 13: 100181. <https://doi.org/10.1016/j.aqrep.2019.100181>.
- Porri, F., T. Jordaan, and C. D. McQuaid. 2008. "Does Cannibalism of Larvae by Adults Affect Settlement and Connectivity of Mussel Populations?." *Estuarine, Coastal and Shelf Science* 79, no. 4: 687–693.
- Pruett, J. L., and M. J. Weissburg. 2019. "Eastern Oysters use Predation Risk Cues in Larval Settlement Decisions and Juvenile Inducible Morphological Defenses." *Marine Ecology Progress Series* 621: 83–94. <https://doi.org/10.3354/meps12998>.
- R Core Team. 2026. R: A Language and Environment for Statistical Computing. (Version 4.4.0) R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Ram, E. J., A. G. Jeffs, and B. M. Skelton. 2026. "The Migratory Behaviour of Juvenile Greenshell Mussels (*Perna canaliculus*)." *Aquaculture, Fish and Fisheries* 6, no. 2: e70142.
- Rato, A., S. Joaquim, D. Matias, and P. C. Hubbard. 2025. "The Roles of Chemical Cues in the Life Cycle of Bivalves: Spawning, Settlement, and Metamorphosis." *Reviews in Aquaculture* 17, no. 1: e13007. <https://doi.org/10.1111/raq.v17.1>.
- Ravalo, L. G. 2024. *Native and Invasive Smooth Shelled Blue Mussels (Mytilus Spp.) in New Zealand: Evolutionary, Biosecurity and Aquaculture Implications*. Open Access Te Herenga Waka-Victoria University of Wellington.
- Redfearn, P., P. Chanley, and M. Chanley. 1986. "Larval Shell Development of Four Species of New Zealand Mussels: (Bivalvia, Mytilacea)." *New Zealand Journal of Marine and Freshwater Research* 20, no. 2: 157–172. <https://doi.org/10.1080/00288330.1986.9516140>.
- Reeder-Myers, L., T. J. Braje, C. A. Hofman, et al. 2022. "Indigenous Oyster Fisheries Persisted for Millennia and Should Inform Future Management." *Nature Communications* 13, no. 1: 1–13. <https://doi.org/10.1038/s41467-022-29818-z>.
- Saavedra, L. M., M. Bastias, P. Mendoza, et al. 2024. "Environmental Correlates of Oyster Farming in an Upwelling System: Implication Upon Growth, Biomass Production, Shell Strength and Organic Composition." *Marine Environmental Research* 198: 106489. <https://doi.org/10.1016/j.marenvres.2024.106489>.
- Sanjayasari, D., and A. Jeffs. 2019. "Optimising Environmental Conditions for Nursery Culture of Juvenile Greenshell Mussels (*Perna canaliculus*)." *Aquaculture* 512: 734338. <https://doi.org/10.1016/j.aquaculture.2019.734338>.

- Schmidlin, S., Y. Treherne, J. Mees, and P. I. Hablützel. 2024. "Planktonic Oyster Larvae Optimize Settlement Decisions in Complex Sensory Landscapes." *bioRxiv*, <https://doi.org/10.1101/2024.11.2028.625415>.
- Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. "NIH Image to ImageJ: 25 Years of Image Analysis." *Nature Methods* 9, no. 7: 671–675. <https://doi.org/10.1038/nmeth.2089>.
- Schulte, D. M., R. P. Burke, and R. N. Lipcius. 2009. "Unprecedented Restoration of a Native Oyster Metapopulation." *Science* 325, no. 5944: 1124–1128. <https://doi.org/10.1126/science.1176516>.
- Sea, M. A., S. F. Thrush, and J. R. Hillman. 2021. "Environmental Predictors of Sediment Denitrification Rates Within Restored Green-Lipped Mussel *Perna canaliculus* Beds." *Marine Ecology Progress Series* 667: 1–13. <https://doi.org/10.3354/meps13727>.
- Skelton, B. M., W. J. McKay, and A. G. Jeffs. 2021. "Evaluation of a Floating Upwelling System for Nursery Culture of the Greenshell Mussel (*Perna canaliculus*)." *Aquaculture Research* 52, no. 8: 3649–3659. <https://doi.org/10.1111/are.15210>.
- Skelton, B. M., M. Múgica, L. N. Zamora, N. J. Delorme, J. A. Stanley, and A. G. Jeffs. 2024. "Nutritional Condition of Wild and Hatchery-Reared, Green-Lipped Mussel (*Perna canaliculus*) Spat Used for Aquaculture." *Aquaculture, Fish and Fisheries* 4, no. 1: e145. <https://doi.org/10.1002/aff2.v4.1>.
- South, P. M. 2016. "An Experimental Assessment of Measures of Mussel Settlement: Effects of Temporal, Procedural and Spatial Variations." *Journal of Experimental Marine Biology and Ecology* 482: 64–74. <https://doi.org/10.1016/j.jembe.2016.05.002>.
- South, P. M., O. Floerl, and A. G. Jeffs. 2017. "Differential Effects of Adult Mussels on the Retention and Fine-Scale Distribution of Juvenile Seed Mussels and Biofouling Organisms in Long-Line Aquaculture." *Aquaculture Environment Interactions* 9: 239–256. <https://doi.org/10.3354/aei00230>.
- South, P. M., O. Floerl, and A. G. Jeffs. 2020. "Magnitude and Timing of Seed Losses in Mussel (*Perna canaliculus*) Aquaculture." *Aquaculture* 515: 734528. <https://doi.org/10.1016/j.aquaculture.2019.734528>.
- Stead, D. H. 1971. *A Preliminary Survey of Mussel Stocks in Pelorus Sound*. New Zealand Marine Department.
- Steeves, L. E., R. Filgueira, T. Guyondet, J. Chassé, and L. Comeau. 2018. "Past, Present, and Future: Performance of Two Bivalve Species Under Changing Environmental Conditions." *Frontiers in Marine Science* 5: 184. <https://doi.org/10.3389/fmars.2018.00184>.
- Swales, A., M. M. Gibbs, S. Handley, et al. 2021. *Sources of Fine Sediment and Contribution to Sedimentation in the Inner Pelorus Sound/Te Hoire*. NIWA.
- Tamburri, M. N., M. W. Luckenbach, D. L. Breitburg, and S. M. Bonniwell. 2008. "Settlement of *Crassostrea ariakensis* Larvae: Effects of Substrate, Biofilms, Sediment and Adult Chemical Cues." *Journal of Shellfish Research* 27, no. 3: 601–608. [https://doi.org/10.2983/0730-8000\(2008\)27%5B601:Socale%5D2.0.Co;2](https://doi.org/10.2983/0730-8000(2008)27%5B601:Socale%5D2.0.Co;2).
- Temmink, R. J. M., C. Angelini, G. S. Fivash, et al. 2021. "Life Cycle Informed Restoration: Engineering Settlement Substrate Material Characteristics and Structural Complexity for Reef Formation." *Journal of Applied Ecology* 58, no. 10: 2158–2170. <https://doi.org/10.1111/1365-2664.13968>.
- Theuerkauf, S. J., B. J. Puckett, and D. B. Eggleston. 2021. "Metapopulation Dynamics of Oysters: Sources, Sinks, and Implications for Conservation and Restoration." *Ecosphere* 12, no. 7: e03573. <https://doi.org/10.1002/ecs2.3573>.
- Thurstan, R. H., H. McCormick, J. Preston, et al. 2024. "Historical Dataset Details the Distribution, Extent and Form of Lost *Ostrea Edulis* Reef Ecosystems." *Scientific Data* 11, no. 1: 1198. <https://doi.org/10.1038/s41597-024-04048-8>.
- Toone, T. A., E. D. Benjamin, S. Handley, A. Jeffs, and J. R. Hillman. 2022. "Expansion of Shellfish Aquaculture Has No Impact on Settlement Rates." *Aquaculture Environment Interactions* 14: 135–145. <https://doi.org/10.3354/aei00435>.
- Toone, T. A., E. D. Benjamin, J. R. Hillman, S. Handley, and A. Jeffs. 2023a. "Multidisciplinary Baselines Quantify a Drastic Decline of Mussel Reefs and Reveal an Absence of Natural Recovery." *Ecosphere* 14, no. 3: e4390. <https://doi.org/10.1002/ecs2.v14.3>.
- Toone, T. A., E. D. Benjamin, J. R. Hillman, and A. Jeffs. 2024. "Assisted Juvenile Recruitment Faces Barriers as a Mussel Restoration Technique." *Aquatic Conservation: Marine and Freshwater Ecosystems* 34, no. 12: e70029. <https://doi.org/10.1002/aqc.70029>.
- Toone, T. A., J. R. Hillman, E. D. Benjamin, S. Handley, and A. Jeffs. 2023b. "Out of Their Depth: The Successful use of Cultured Subtidal Mussels for Intertidal Restoration." *Conservation Science and Practice* 5, no. 4: e12914. <https://doi.org/10.1111/csp2.v5.4>.
- Toone, T. A., J. R. Hillman, E. D. Benjamin, S. Handley, and A. Jeffs. 2023c. "Provision of Early Mussel Life Stages via Macroalgae Enhances Recruitment and Uncovers a Novel Restoration Technique." *Journal of Experimental Marine Biology and Ecology* 566: 151919. <https://doi.org/10.1016/j.jembe.2023.151919>.
- Toone, T. A., J. R. Hillman, P. M. South, E. D. Benjamin, S. Handley, and A. G. Jeffs. 2023d. "Bottlenecks and Barriers: Patterns of Abundance in Early Mussel Life Stages Reveal a Potential Obstacle to Reef Recovery." *Aquatic Conservation: Marine and Freshwater Ecosystems* 33, no. 8: 810–821. <https://doi.org/10.1002/aqc.3979>.
- Toupoint, N., L. Gilmore-Solomon, F. Bourque, et al. 2012. "Match/Mismatch Between the *Mytilus edulis* Larval Supply and Seston Quality: Effect on Recruitment." *Ecology* 93, no. 8: 1922–1934. <https://doi.org/10.1890/11-1292.1>.
- Ulrich, S. C., and S. J. Handley. 2020. "From Clean and Green to Brown and Down: A Synthesis of Historical Changes to Biodiversity and Marine Ecosystems in the Marlborough Sounds, New Zealand." *Ocean & Coastal Management* 198: 105349. <https://doi.org/10.1016/j.ocecoaman.2020.105349>.
- van der Heide, T., E. Tielens, E. M. van der Zee, et al. 2014. "Predation and Habitat Modification Synergistically Interact to Control Bivalve Recruitment on Intertidal Mudflats." *Biological Conservation* 172: 163–169. <https://doi.org/10.1016/j.biocon.2014.02.036>.
- Vignier, J., O. Champeau, J. Atalah, et al. 2025. "Land-Derived Metals Impact the Survival and Settlement of Larval Mussels." *Environmental Pollution* 367: 125675. <https://doi.org/10.1016/j.envpol.2025.125675>.
- Wilcox, M., and A. Jeffs. 2017. "Is Attachment Substrate a Prerequisite for Mussels to Establish on Soft-Sediment Substrate?" *Journal of Experimental Marine Biology and Ecology* 495: 83–88. <https://doi.org/10.1016/j.jembe.2017.07.004>.
- Wilcox, M., and A. Jeffs. 2019. "Impacts of Sea Star Predation on Mussel Bed Restoration." *Restoration Ecology* 27, no. 1: 189–197. <https://doi.org/10.1111/rec.2019.27.issue-1>.
- Wilcox, M., S. Kelly, and A. Jeffs. 2018. "Ecological Restoration of Mussel Beds Onto Soft-Sediment Using Transplanted Adults." *Restoration Ecology* 26, no. 3: 581–590. <https://doi.org/10.1111/rec.12607>.
- Wilcox, M., S. Kelly, and A. Jeffs. 2020. "Patterns of Settlement Within a Restored Mussel Bed Site." *Restoration Ecology* 28, no. 2: 337–346. <https://doi.org/10.1111/rec.v28.2>.
- Wood, G. V., K. Filbee-Dexter, M. A. Coleman, et al. 2024. "Upscaling Marine Forest Restoration: Challenges, Solutions and Recommendations From the Green Gravel Action Group." *Frontiers in Marine Science* 11: 1364263. <https://doi.org/10.3389/fmars.2024.1364263>.
- WorRMS Editorial Board. 2026. "World Register of Marine Species." Accessed August 19, 2026. <https://www.marinespecies.org>.

- Wu, W., I. Anderson, and A. G. Jeffs. 2025. "The Role of Substrata Width and Millimeter Scale Surface Micro-Structure in the Attachment of Juvenile Mussels." *Aquaculture* 595: 741593. <https://doi.org/10.1016/j.aquaculture.2024.741593>.
- Wu, W., C. J. Lundquist, and A. G. Jeffs. 2025. "Determining the Significance of Pelagic Versus Juvenile Dispersal of Larvae in a Coastal Mussel." *Science of the Total Environment* 969: 178940. <https://doi.org/10.1016/j.scitotenv.2025.178940>.
- Yang, Y., Y. P. Wang, S. Gao, et al. 2016. "Sediment Resuspension in Tidally Dominated Coastal Environments: New Insights Into the Threshold for Initial Movement." *Ocean Dynamics* 66, no. 3: 401–417. <https://doi.org/10.1007/s10236-016-0930-6>.
- Zhao, Z. Y., J. J. Capelle, J. C. de Smit, et al. 2024. "Boosting Efficiency of Mussel Spat Collection for Ecological Sustainability: Identifying Critical Drivers and Informing Management." *Journal of Applied Ecology* 61, no. 7: 1691–1702. <https://doi.org/10.1111/1365-2664.14696>.
- zu Ermgassen, P. S., K. Bonačić, P. Boudry, et al. 2020. "Forty Questions of Importance to the Policy and Practice of Native Oyster Reef Restoration in Europe." *Aquatic Conservation: Marine and Freshwater Ecosystems* 30, no. 11: 2038–2049. <https://doi.org/10.1002/aqc.3462>.
- Zu Ermgassen, P. S. E., M. D. Spalding, B. Blake, et al. 2012. "Historical Ecology With Real Numbers: Past and Present Extent and Biomass of an Imperilled Estuarine Habitat." *Proceedings of the Royal Society B: Biological Sciences* 279, no. 1742: 3393–3400. <https://doi.org/10.1098/rspb.2012.0313>.

## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Output of fixed effects from a negative binomial generalised linear mixed model examining juvenile green-lipped mussel settlement on coir as a function of treatment, retrieval time and their interaction. **Table S2:** Pairwise comparisons of green-lipped mussel juveniles settled onto coir between Coir and Mussels with coir treatments at three retrieval events, 2, 6 and 16 weeks post-deployment. **Table S3:** Fixed-effect coefficients from the linear mixed-effects model testing the effects of treatment, retrieval month and their interaction on juvenile green-lipped mussel shell length ( $\mu\text{m}$ ). **Table S4:** Type III ANOVA results from a linear mixed-effects model testing the effects of treatment, retrieval month and their interaction on juvenile green-lipped mussel shell length ( $\mu\text{m}$ ).