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Quantifying Mussel Losses From Fish Predation on New Zealand Greenshell Mussel (*Perna canaliculus*) Farms

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ABSTRACT

Fish predation is a severe contributor to mussel losses in aquaculture. Quantifying these losses during the production cycle is a crucial step for developing effective interventions to improve efficiency of mussel aquaculture. Despite frequent anecdotal reports of fish predation in New Zealand's Greenshell mussel (*Perna canaliculus*) industry, the contribution of predation to mussel losses remains unclear. Fish predation is thought to be more severe in the early stages of mussel production due to the vulnerability of juvenile mussels but is difficult to measure due to other causes of mussel losses. An experimental caging method was used to determine the extent of fish predation on Greenshell farms. The use of this caging method during initial seeding (0.9–8 mm shell length—SL), juvenile (25–34 mm SL), inter-seeding (39–48 mm SL) and final re-seeding (43–54 mm SL) of mussels in the Firth of Thames in northern New Zealand found losses due to predation of up to 93% in juvenile mussels over 67 days. In contrast, predation did not contribute significantly to mussel losses over 2 months following initial seeding, inter-seeding or final-re-seeding production stages, despite losses of mussels reaching 94% and 33% after initial and final re-seeding, respectively. The results indicate that at <8 and >39 mm SL, Greenshell mussels may be resistant or less attractive to fish predators. Other causes of Greenshell mussel losses at these stages of production need to be identified, whereas fish predation of mussels at 8–25 mm SL needs to be further investigated.

1 | Introduction

The success of the global mussel aquaculture is heavily reliant on the settlement, survival and retention of wild juvenile mussels, also known as seed or spat (Carl et al. 2012; South et al. 2022). In most mussel-farming locations around the world, the supply of wild spat for initiating aquaculture production is highly variable and increasingly constrained due to environmental factors and management restrictions, such as catch controls and quotas (Alfaro et al. 2011; Buchanan 1999; Jeffs et al. 2018; Kamermans et al. 2002; Kamermans and Capelle 2019; Walter and Liebezeit 2003). The natural vagaries in supplies of wild spat to initiate the mussel-farming production cycle commonly lead to disruptions

and declines in mussel aquaculture production output (Avdelas et al. 2021; Capelle, Scheiberlich, et al. 2016; Fuentes et al. 1998; Parappurathu et al. 2021; South et al. 2022). For example, European mussel aquaculture declined by around 20% between 1990 and 2016 due to various factors, which included issues with natural mussel spat supply, while during this same period global mussel production output increased overall (Avdelas et al. 2021). Although spat losses are very common in early production stages, other inefficiencies in mussel aquaculture also occur (i.e., losses of both juveniles and adults) later in the production cycle when spat and juveniles are more established, but these tend to be much less impactful in terms of the total numbers of mussels that are lost from production (Skelton and Jeffs 2022).

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In many cases, the exact causes of mussel losses are poorly understood and can change depending on when they occur in the production cycle (South et al. 2022). Predation by fish is believed to be a significant cause of losses at all stages of the production cycle for many mussel species, especially in those farming regions using suspended aquaculture methods (Stobart, Jeffs, Skelton 2025). The presence of these farming structures in coastal areas creates habitat that is attractive to fish, with mussel farm habitats typically containing around 1.6 times greater abundance of fish than nearby reference areas of natural habitat (Theuerkauf et al. 2022). For example, mussel farm habitats in the Adriatic Sea have been shown to contain 33 times greater abundance of fish than the average of three nearby reference areas of natural habitat (Šegvić-Bubić et al. 2011), whereas mussel farm habitats in New Zealand have been found to contain around 3.4 times greater abundance of fish (Underwood and Jeffs 2023). Mussel farm structures provide protection for fish in the water column, whereas biofouling organisms and the cultured mussels on the farm infrastructure tend to enhance productivity, creating additional feeding opportunities for fish (Costa-Pierce and Bridger 2002; D'Amours et al. 2008). These farms serve as important habitats for small benthic and demersal species, such as triplefin (Tripterygiidae) and spotty (*Notolabrus celidotus*), which have been observed settling as larvae and establishing in high densities within Greenshell mussel (*Perna canaliculus*) farms in New Zealand (Carbines 1993; Morrissey et al. 2006; Stobart, Jeffs, Hillman, et al. 2025; Underwood and Jeffs 2023). Similarly, larger demersal predators, such as gilthead seabream (*Sparus aurata*) in the Mediterranean and Australasian snapper (*Chrysophrys auratus*), in the Firth of Thames, New Zealand, have been documented in extremely high densities within mussel farms, likely attracted by the readily available food source provided by the cultured bivalves (Glamuzina et al. 2014; Richard et al. 2020; Šegvić-Bubić et al. 2011; Stobart, Jeffs, Hillman, et al. 2025; Underwood and Jeffs 2023; Underwood et al. 2023).

Predation by fish has been reported in Europe where exposure of line-caught Mediterranean mussel (*Mytilus galloprovincialis*) spat (i.e., mussels of 1–20 mm shell length [SL]) to fish predation resulted in a reduction in recruitment between 38% and 58% among different spat collector types (Peteiro et al. 2010). Likewise, predation of *M. galloprovincialis* from farm longlines by fish at the inter-seed to final-re-seeding stages of aquaculture production (i.e., mussels of 34–58 mm SL) can reach anywhere between 54% and 90% in Croatia and France, respectively (Richard et al. 2020; Šegvić-Bubić et al. 2011). Predation by fish has also been reported in raft culture of blue mussels, *Mytilus edulis* (Australia), and green mussels, *Perna viridis* (India), and in longline culture of Greenshell mussels (New Zealand) (Appukuttan 1980; Hayden 1995; MacIntyre et al. 1977; Soundararajan et al. 1988; Stobart, Jeffs, Hillman, et al. 2025). However, there remains a poor understanding of the size and quantities of cultured mussels that are lost from aquaculture operations through predation by fish, as well as the identity and predatory behaviour of the fish species responsible (e.g., fish picking off and consuming individual mussels, or stripping entire mussel-growing lines; Bartsch et al. 2005; Crooks 2002; Denny and Schiel 2001; Hayden 1995; Osman and Whitlatch 1998; Peteiro et al. 2010; Pita et al. 2002; Šegvić-Bubić et al. 2011).

This lack of knowledge is in part due to the difficulties in attributing the loss of mussels from farms to predation by fish versus other possible causes, such as natural mortality, migration and disease (Castinel et al. 2019). Physical exclusion is used in several shellfish farming regions of the world to exclude mobile predators from consuming farm stock. For example, exclusion nets have been used in some European mussel-farming regions to deter seabream predation on spat-collectors and culture longlines (Peteiro et al. 2010; Richard et al. 2020), with up to 85% of mussel farmers in the French Mediterranean using nets to protect mussels from fish (Gervasoni and Giffon 2016; Richard et al. 2020). Hence, physical exclusion provides a useful avenue for experimentally isolating the specific impact of fish predators on mussel farm losses. However, employing physical exclusion methods, like experimental caging in marine ecological studies, also requires measures to mitigate any potential artefacts associated with the presence of the cages. For example, partial cages can be used to identify caging artefacts while still allowing some predator access (Como et al. 2006; Connell 1997). This approach of experimentally using full and partial cage exclusion has previously been applied successfully to isolate the impacts of predation by fish from other potential sources of losses of early juvenile Greenshell mussels from farms in southern New Zealand (Hayden 1995).

Extensive areas of coastal mussel farms in New Zealand produce a total of around 100,000 t a year of the green-lipped mussels, also known as Greenshell, when commercially cultured (AQNZ 2020; Jeffs et al. 1999). The contribution of fish predation to mussel losses during Greenshell farming is poorly understood; however, mussel farmers in the Firth of Thames in northern New Zealand report extensive and consistent losses of significant quantities of mussels at all stages of production, but especially during the period immediately after seeding (<1 mm SL) or re-seeding juvenile mussels (10–20 mm SL) onto their farms. For example, one mussel aquaculture company estimates the consistent losses of mussels from farms due to fish predation amount to around NZ\$5 million in lost production a year (Stobart, Jeffs, Hillman, et al. 2025).

Experimental exclusion of fish from a Greenshell mussel farm in the Marlborough region of southern New Zealand was found to significantly reduce losses of mussel spat of 9–15 mm SL by up to 100% (Hayden 1995). Complete loss of mussels from lines with attached spat was observed for both partially caged and uncaged spat lines between 24 h and 14 days after deployment, whereas the number of mussel spat on fully caged lines was maintained (Hayden 1995). Fish predation on mussels was found to be site-specific with some evidence that fish were targeting the larger mussels (>12 mm SL) which protruded past the smaller mussels (<2 mm SL) on the spat lines. More recent studies in New Zealand have used remote underwater video (RUV) to confirm that fish, especially Australasian snapper, were biting at the mussel-growing lines (Stobart, Jeffs, Hillman, et al. 2025) and that mussels form a significant portion of the diet of snapper living in mussel farms (Underwood et al. 2024; Underwood et al. 2023). In addition, a coastal fish species, parore (*Girella tricuspidata*), has been identified as a common inhabitant of mussel farms with the potential to contribute to losses of spat from recently seeded spat farms, where genetic analyses of gut contents show they consume mussels, possibly as a result of consuming the macroalgae that

is encrusted with mussel spat, which is commonly used to seed mussel farms (Martis-Geor 2023; Stobart, Jeffs, Hillman, et al. 2025). These results indicate the potential for consistently severe impacts of fish predation during the early stages of mussel aquaculture that are aligned with the anecdotal reports from the mussel farmers; however, they do not provide direct evidence of this phenomenon or a measure of the extent of the predation.

This study used experimental caging methods to measure the extent of predation by fish on Greenshell mussels as a possible cause of extensive losses of mussels from farms in northern New Zealand. To attempt to determine the stage of mussel production when mussels were most vulnerable to predation, four separate predator exclusion experiments were conducted in conjunction with commercial mussel-farming activities at (1) the initial seeding, (2) juvenile, (3) inter-seeding and (4) final-re-seeding production stages (i.e., mussel sizes ranging from 0.9 to 8, 25 to 34, 30 to 50 and 40 to 60 mm SL, respectively).

2 | Materials and Methods

2.1 | Study Sites and Mussel Spat Sources

To measure the loss of mussels from commercial Greenshell farms, four separate field experiments were conducted for four size classes of mussels each at one of four commercial coastal mussel farm sites in the Firth of Thames in northern New Zealand. To ensure the results of this study were commercially relevant and to avoid prohibitive costs of conducting the study independently of industry support, the experiments for this study were integrated with commercial mussel-farming activities. A consequence of this approach to the research was an inability to direct the location, timing and size classes of mussels that were deployed for experiments, as these factors were controlled by industry production requirements. In New Zealand, farmed mussels tend to be seeded within a specific period, which means that different size classes are present at different locations and times of the year instead of all at once at a single site. Moreover, different sites are used for growing mussels of different sizes, as their tolerance to more exposed coastal conditions increases with the size of the mussels. As a result, it was not possible to run experiments for all mussel size classes at the same time in the same place with industry support. Consequently, separate experiments examining fish predation in different mussel size classes occurred at different farm locations and times of year. This pragmatic approach enabled the research to proceed but potentially confounds any comparisons among the individual experiments. Hence, the experiments are all analysed independently, and where the results from the different experiments are compared among the experiments for individual size classes, the proviso of the possible confounding effects needs to be taken into consideration. Despite this constraint, the study design effectively provides a preliminary measure of fish predation for a range of industrially relevant mussel size classes under real commercial conditions, yielding pertinent insights into patterns expected in an industry context.

Experiment 1 was conducted on a recently seeded spat farm in the northeast of Hautapu Channel (36°44'12.88" S, 175°26'40.24" E) (Figure 1). The farm was first seeded on 26 July 2022 with wild spat

attached to drift seaweed and other material that was harvested from Ninety Mile Beach (NMB), which is located at the northern tip of the North Island of New Zealand (Figure 1; Hickman 1982; Jeffs et al. 1999). The harvested spat material was transferred to the dropper lines of the longline farm and held in place with the use of an elasticated cotton socking, known as mussock, to hold the seed mussels in place until they attached to the line with byssus threads, a process known as re-seeding a dropper line. The mussock is also thought to provide some protection from predators for the unattached mussels. Experiment 1 was initiated on this farm 3 weeks after seeding (i.e., 15 August 2022) when mussels had reached an average size of 0.9 mm SL. Experiment 1 concluded after 12 weeks on 17 October 2022.

Experiment 2 was conducted on a mussel farm at Esk Point (36°48'27.82" S, 175°26'8.65" E; Figure 1) which was seeded with spat harvested from NMB on 22 August 2022. Experiment 2 was deployed 25 weeks later (i.e., 10 February 2023), by which time the spat had reached an average size of 25 mm SL and had formed strong byssus attachment to the dropper line, and the mussock used during the initial seeding had fully degraded. Experiment 2 concluded after 10 weeks on 18 April 2023.

Experiment 3 was conducted adjacent to Experiment 1 at a farm site in the Hautapu Channel (36°44'25.36" S, 175°26'56.06" E) and Experiment 4 at Wilson Bay (36°58'50.31" S, 175°24'7.19" E; Figure 1). The mussels used in both the experiments were sourced from Aotea Harbour on the west coast of the North Island (Figure 1) where they were caught on polypropylene spat collecting rope which was then stripped from the catching rope and seeded onto dropper lines and encased in mussock.

The first re-seeding took place on 17 May 2022 at the Hautapu Channel (b) mussel farm (Figure 1). Experiment 3 was deployed here 20 weeks later (i.e., 29 September 2022), at which time the mussels had reached an average size of 38 mm SL (± 0.2 SE) and the mussock had completely degraded. The experiment concluded after 4 weeks on 29 November 2022.

In preparation for Experiment 4, mussels from the Hautapu Channel (b) mussel farm, which were not involved in Experiment 3, were stripped from their dropper line and re-seeded at a Wilson Bay mussel farm on 27 October 2022 (36°58'50.31" S, 175°24'7.19" E; Figure 1). Experiment 4 was set up on 7 November 2022, when the mussels had grown to an average size of 43.6 mm SL (± 0.1 SE), the mussock had not yet completely degraded, and biofouling had not established on the mussels and dropper line. Experiment 4 concluded on 6 January 2023.

2.2 | Experimental Design

To assess the extent of losses of mussels due to fish predation from mussel dropper lines, three experimental treatments were applied to 1.5 m lengths of dropper line: (1) enclosure with a full mesh cage to exclude fish predation, (2) enclosure with a partial mesh cage that allowed fish predation but controlled for possible effects of the presence of a mesh cage and (3) no enclosure of the dropper line, which served as a control. The full mesh cages consisted of a 1.5 m cylinder (250 mm ϕ) made of 25 mm square plastic mesh with mesh ends to each cylinder that were fabricated so that they

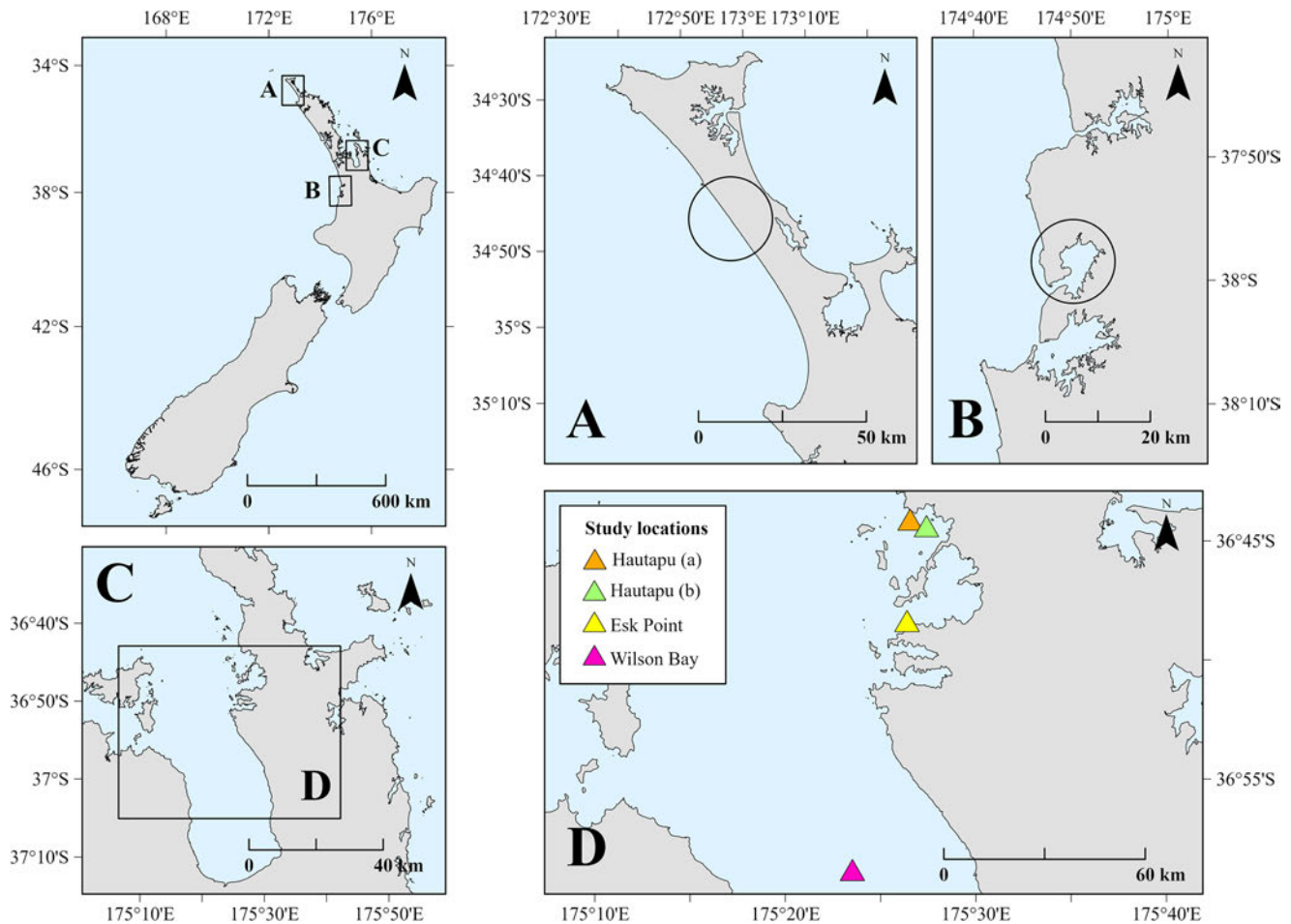


FIGURE 1 | Location of the two sites where mussel spat were sourced: (A) Ninety Mile Beach (Experiments 1 and 2) and (B) Aotea Harbour (Experiments 3 and 4). (C) Location of the Firth of Thames in northern New Zealand and (D) location of the three mussel farms that were used as study sites for deploying four fish predator exclusion experiments. Orange triangle: Hautapu Channel (a) (0.9–8 mm SL mussels; Experiment 1), green triangle: Hautapu Channel (b) (38–48 mm SL mussels; Experiment 3), yellow triangle: Esk Point (25–35 mm SL mussels; Experiment 2) and pink triangle: Wilson Bay (43–54 mm SL mussels; Experiment 4).

could be easily attached around dropper lines using cable ties. The partial mesh cages were identical to full mesh cages, except that six rectangular panels (measuring $125 \times 250 \text{ mm}^2$ each) were randomly cut out of the mesh cylinder to provide access to potential predators while also controlling for any potential artefacts due to the presence of the mesh cage (Figure 2).

At the outset of each experiment, a length of at least 20 m of mussel-encrusted dropper line was randomly selected and divided into 50 (Experiment 1), 39 (Experiment 2), 32 (Experiment 3) and 47 (Experiment 4) $\sim 1.5 \text{ m}$ replicate lengths. All attached mussels within each replicate sample were counted and measured to determine the initial mussel density and size. The results from replicate samples at the outset of each experiment were randomly assigned to treatments and depths for the purposes of maintaining balance in the replication for subsequent statistical analyses. Nine replicates of each of the two cage treatments were then randomly attached to a 1.5 m section of the continuous seeded dropper line at each of two depths (0–5 and 5–10 m), totalling 18 replicates of each cage type (Figure 2). Triplicate replicates of each treatment-depth combination were sampled at approximately 3-week intervals following deployment.

On each sampling day, 3 replicates of each of the 3 treatments (i.e., 3 full cages, 3 partial cages and 3 controls at each of the 2 depths for a total of 18 samples) were randomly selected and recovered to determine the density and sizes of the remaining mussels. This was repeated for three sampling days for each experiment, at different intervals due to logistic constraints (Table 1).

Due to the differing sizes of mussels in Experiment 1 compared to Experiments 2, 3 and 4, different sampling protocols were used to determine seeding density and the sizes of mussels still attached to the sampled dropper line.

2.2.1 | Experiment 1 (0.9 mm SL)

For each sampling day (i.e., Days 21, 43 and 64), each 1.5 m length of sampled dropper line was divided into 30 cm sections for ease of analysis. For each 30 cm section, any remaining mussock and macroalgal material that would have accompanied the wild spat at seeding was carefully separated from the dropper line and rinsed with freshwater over a $200 \mu\text{m}$ sieve to detach and collect any mussel spat. Careful inspection and removal of spat

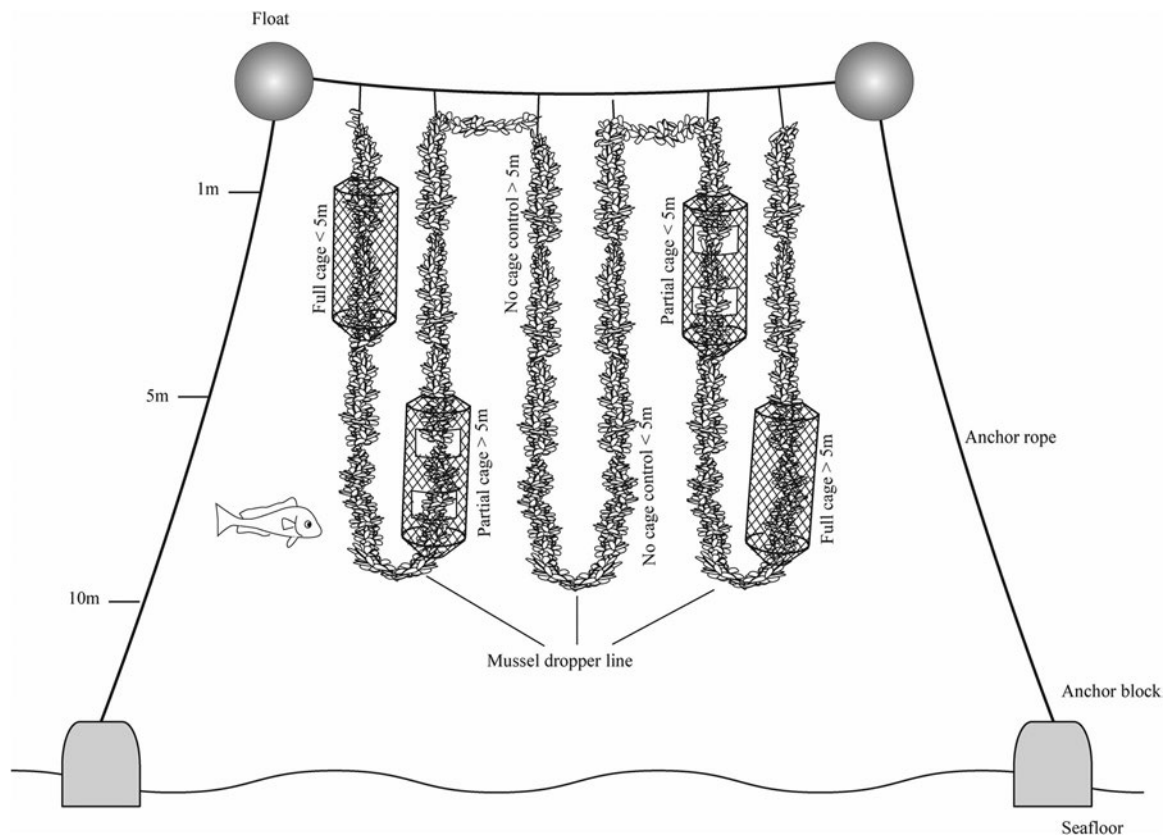


FIGURE 2 | Schematic diagram of the experimental design with three treatments: full and partial mesh cages and controls without mesh cages, deployed on dropper lines at two depths (0–5 and 5–10 m).

TABLE 1 | Summary of sampling locations, initial mussel size (mm shell length [SL]) and the timing of sampling Days 1–3 for each of the four experiments.

Experiment	Sampling location	Mussel size (mm SL)	Sampling days		
			1	2	3
1	Hautapu Channel (a)	0.93 (± 0.013 SE)	21	43	64
2	Esk Point	24.5 (± 0.03 SE)	21	42	67
3	Hautapu Channel (b)	38.0 (± 0.2 SE)	20	41	63
4	Wilson Bay	43.5 (± 0.09 SE)	21	43	60

with tweezers were used to ensure all spat were removed from the line. The detached spat were uniformly distributed in a large petri dish, and counts were subsampled within five selected 4 cm² areas. These counts were then averaged and scaled up to represent the total spat count per dish, which was further extrapolated to estimate spat density per metre still attached to the residual macroalgae, mussock and dropper line to estimate spat density per metre of dropper line.

Following the detachment of all spat, the mussock and macroalgae were separated from each other and air-dried for 24 h at 50°C. The dry weight of mussock and macroalgae was recorded and used to calculate their dry weight per metre of dropper line.

2.2.2 | Experiments 2 (25 mm SL), 3 (38 mm SL) and 4 (44 mm SL)

For each sampling day, the sampled 1.5 m dropper lines were returned to the laboratory and cut into 30 cm sections, and at least three of these sections per line were randomly selected for analyses. For each selected section of line, all mussels were removed by hand and then counted, and the SL of each mussel was measured using image analysis of digital photographs (ImageJ Software). The resulting counts from each replicate were then used to determine the mean number of mussels per metre of line. Any mussock remaining on each section of line in Experiment 4 was quantified by rinsing in freshwater and placing in the drying oven at 60°C for 24 h before determining the dry weight.

TABLE 2 | Summary of the post hoc power analyses for additive and interaction models for each of the four experiments.

Experiment	Model	Sampling day	Treatment	Depth	Three-way interaction
1	Interaction	0	0	0	5.3
	Additive	100	40	16	NA
2	Interaction	0	0	0	30
	Additive	100	96	51	NA
3	Interaction	0	0	0	37.6
	Additive	52.4	18	8.6	NA
4	Interaction	0	0	0	8.1
	Additive	100	47.4	6.5	NA

2.3 | Statistical Analyses

Mussel densities were transformed to relative values to standardise comparisons among treatments and depths. Relative density was calculated by dividing each replicate by the overall mean density observed on Day 0 among all droppers. This approach enabled changes in mussel density to be interpreted in proportion to initial conditions, while accounting for variability in baseline densities among droppers.

Because replicate numbers differed among experiments, due to (1) variation in sampled rope length at the outset of the experiment, (2) sample loss during the experiment and (3) differences in laboratory sampling protocols between Experiments 1 and 2–4, the within-group degrees of freedom also varied among experiments.

For each experiment, a linear mixed-effects model (Lmer) was constructed to analyse the relationship between the mean relative change of mussels per metre of dropper line and the fixed effects of treatment, depth, sampling day and their interactions. A random intercept for each unique identifier or ‘dropper’ was included to account for potential within-dropper correlation. After fitting the model, an analysis of variance (ANOVA) was performed on the Lmer object to assess the significance of the fixed effects and their interactions. For each ANOVA, the assumptions of normality and homogeneity of variance were examined by plotting the distributions of residuals and the residuals versus means. A post hoc power analysis was subsequently performed using a simulation on the basis of the observed effect sizes and variance structure of the fitted model. This analysis aimed to determine the probability of detecting effects of the observed magnitude under the existing experimental design. Simulations were run with 1000 iterations, while holding the structure of the random effects constant. Therefore, power simulations indicated insufficient sensitivity to reliably detect interaction effects under the current experimental designs (Table 2).

Bayesian simulation analysis indicated that the models could only reliably detect three-way interaction effects when they corresponded to a decline in relative mussel density of at least 40% in Experiments 1, 3 and 4 and 20%–40% in Experiment 2 from Day 0. Therefore, only moderate-to-large changes in mussel density would be reliably detected under the current experimental design;

however, such magnitudes of losses were anecdotally reported by mussel farmers operating in the Firth of Thames.

Consequently, additive models with the same fixed and random effect structure were retained as they provided a more stable and interpretable basis for inference given the limitations in power. For each ANOVA, the assumptions of normality and homogeneity of variance were examined by plotting the distributions of residuals and the residuals versus means.

Where significant main effects were observed, post hoc pairwise comparisons were conducted using Tukey-adjusted estimated marginal means (emmeans) derived from the fitted linear mixed-effects model to evaluate comparisons among treatments, depths or days. To assess the magnitude of pairwise differences, effect sizes were calculated as Hedge’s g using the effectsize package.

The interaction model was retained to analyse the relationship between the mean dry weight of mussock and algae per metre of dropper line and determine any differences in the mean SL of mussels remaining attached to the dropper line.

A chi-square test of goodness-of-fit was used to determine whether at the end of each experiment the frequencies of mussels in serial size classes differed among the treatments for each of the two depths (data pooled for replicates for each treatment and depth combination). Serial size classes of mussels were adjusted so that at least 5% of the data fell into each size class to satisfy the requirements of the statistical test: Experiment 1 = <4, 5–6, 7–8, 8–9, >9 mm SL; Experiment 2 = <25, 26–30, 31–35, 36–40, >40 mm SL; Experiment 3 = <25, 26–35, 36–45, 46–55, 56–65, >65 mm SL and Experiment 4 = <40, 41–50, 51–60, >60 mm SL. Deviations from expected frequencies in the distribution of mussel size classes among treatments and depths were confirmed using adjusted residuals.

3 | Results

3.1 | Mussel Losses

At the outset of the experiment (0 days), the mean density of mussels averaged among treatments and depths attached to the dropper line was 57,205 mussels m^{-1} (± 5212 SE) in Experiment 1,



FIGURE 3 | Photographs taken on 3 March 2023 of mussel farm dropper lines from Experiment 2 at Esk Point holding mussels of 25–30 mm shell length showing the effects of fish predation on mussel dropper lines 21 days since the outset of the experiment: (A) intact dropper line from caged treatment, (B) section of control dropper line recently stripped of mussels by predation and (C) control dropper line stripped completely bare.

1898 mussels m^{-1} (± 54 SE) in Experiment 2, 216 mussels m^{-1} (± 9 SE) in Experiment 3 and 245 mussels m^{-1} (± 8 SE) in Experiment 4. Mussel density gradually declined over the course of all the experiments except for Experiment 3, where no clear pattern was observed. The algal material used during initial seeding was degraded in all but Experiment 1, and the mussock used for initial seeding and intermediate re-seeding was only intact for Experiments 1 and 4.

All of the retrieved samples from both Experiments 1 and 4 were found to contain torn mussock in both control and partial cage treatments with tears in the mussock of up to 10 cm in length. In Experiments 2, 3 and 4, the retrieved samples from throughout the experimental period were observed to contain the broken umbos of mussel shells remaining attached to the dropper line in both control and partial cage treatments. In both these treatments, there were also some small patches of up to 30 cm in length of dropper line from which mussels were absent, consistent with the pattern of predation by fish observed feeding on mussels from dropper lines (Figure 3; Stobart, Jeffs, Hillman et al. 2025). In Experiment 4, these observations were more distinct in samples from 43 days and once the mussock had fully degraded in all treatments.

In Experiment 3, one full cage from the 0–5 m depth was missing at the final sampling day (i.e., 63 days), most likely lost during industry stripping and re-seeding procedures. In Experiment 4, eight samples were lost during data collection, likely due to tidal currents at the farm site that caused them to break free from their attachment to the seeded dropper line (Table 3), and hence, these were subsequently excluded from the data set.

In Experiment 3, there was a high degree of variability in the sampled density of mussels on the growing lines that was consistent for all treatments which could not have been due to any effect of predation on caged versus partially caged and control treatments (Figure 4). Furthermore, there is no indication of the variability in the sampled density of mussels changing through time for any of the treatments, as might be expected for the partial cage and control treatments if mussels were being removed in discrete areas from the lines due to localised removal from the dropper lines by fish predators. The relatively high variability in the measured density of mussels for all experimental lines occurred at all levels of the experiment, both among samples within individual dropper lines and among dropper lines within treatments. For example, 20 days after deployment of the experiment, at the 0–5 m depth, the average variability (i.e., SE as % of mean) within and between individual dropper lines was 18% and 7%, respectively, for the control treatment, 12% and 9% for partial cages and 16% and 20% for full cages. At the 5–10 m depth, the average variability within and between individual dropper lines was 31% and 29%, respectively, for the control, 23% and 4% for partial cages, and 17% and 21% for the full cages.

Overall, the mean relative change of the density of mussels remaining attached to the dropper lines differed among sampling days in Experiments 1 ($F_{(3,46)} = 34.7$, $p < 0.001$), 2 ($F_{(3,51)} = 17.06$, $p < 0.001$) and 4 ($F_{(3,36)} = 19.2$, $p < 0.001$) but not in Experiment 3 ($F_{(3,47)} = 1.86$, $p = 0.15$; Figure 4). There were no differences observed in the relative change of mussel density between depths in any of the experiments (Experiment 1; $F_{(1,53)} = 0.21$, $p = 0.65$, Experiment 2; $F_{(1,51)} = 3.59$, $p = 0.07$, Experiment 3; $F_{(1,50)} = 0.03$, $p = 0.87$, Experiment 4; $F_{(1,44)} = 0.03$, $p = 0.86$). The mean

TABLE 3 | Summary of missing samples from each sampling day in each treatment at each depth in Experiment 4.

Sampling day	Depth (m)	Treatment		
		Control	Partial cage	Full cage
1 (22)	0–5	0/3	1/3	0/3
	5–10	0/3	0/3	1/3
2 (43)	0–5	0/3	0/3	0/3
	5–10	0/3	2/3	0/3
3 (61)	0–5	1/3	2/3	0/3
	5–10	0/3	1/3	0/3

Bolded entries indicate missing samples.

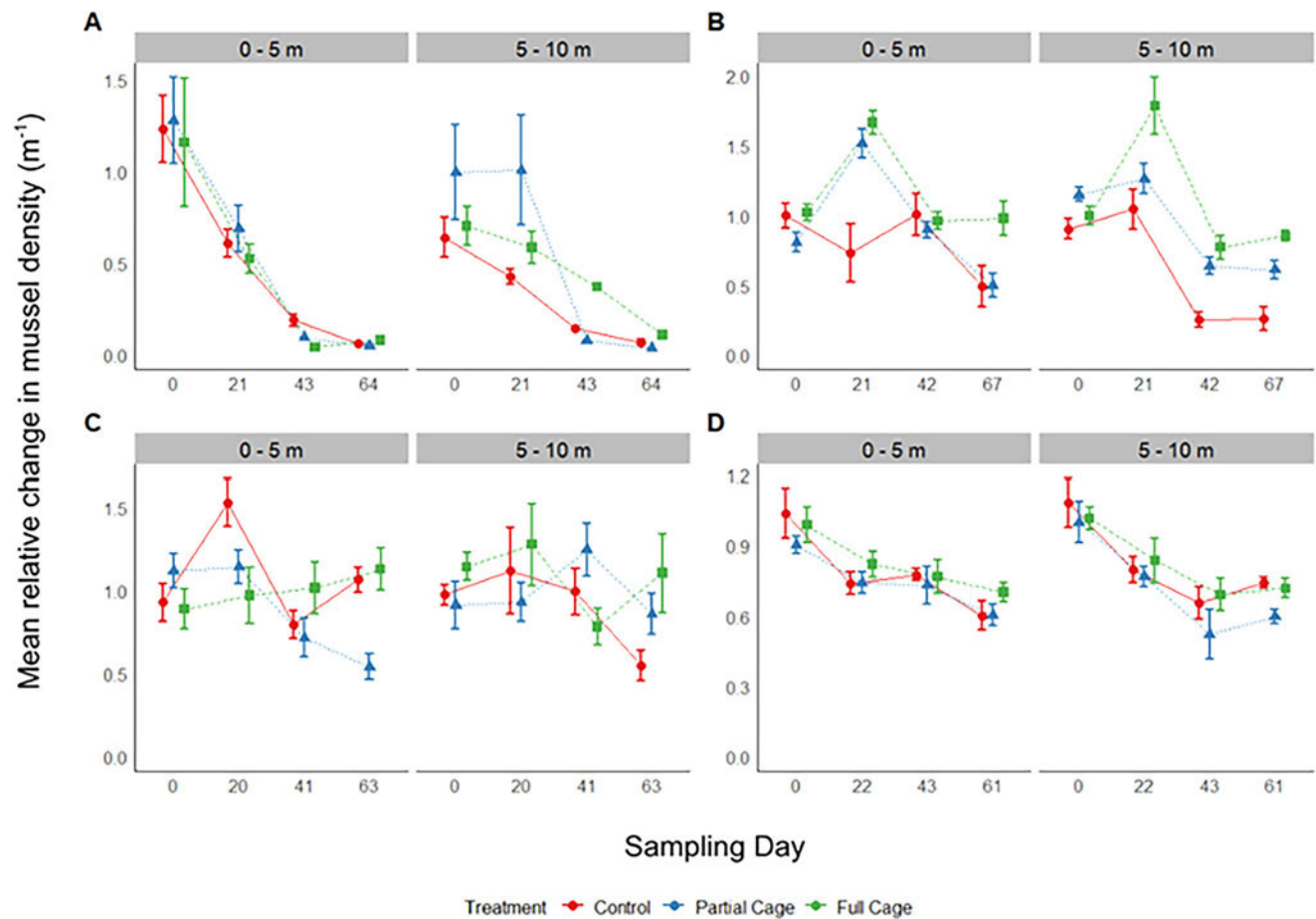


FIGURE 4 | Mean relative change in the density of mussels ($\text{m}^{-1} \pm \text{SE}$) on dropper lines for each of three fish predator treatments (i.e., control—no cage, partial cage and full cage) at each of two depths (0–5 and 5–10 m) for each of the four sampling days in (A) Experiment 1, (B) Experiment 2, (C) Experiment 3 and (D) Experiment 4. Means are the raw means of relative change calculated from raw densities. Error bars are jittered to prevent overlap.

relative change of the density of mussels remaining attached to the dropper lines differed among treatments in Experiment 2 ($F_{(2, 51)} = 7.89$, $p < 0.01$) but not in Experiments 1 ($F_{(2, 53)} = 1.7$, $p = 0.19$), 3 ($F_{(2, 50)} = 0.49$, $p = 0.62$) and 4 ($F_{(2, 41)} = 1.7$, $p = 2.0$).

Although model-based estimates did not detect statistical differences among treatments, the observed means suggest that losses

to predation by fish ranged between 2% and 22% in Experiment 1, 0% and 56% in Experiment 3, and 0% and 12% in Experiment 4 (Table 4).

In Experiment 2, the model estimated losses to predation by fish to reach 38%, but the observed means ranged between 0% and 93%.

TABLE 4 | Summary of the overall percentage of mussel losses and the percentage of mussel losses attributed to predation by fish (control—full cage losses) for each of the four experiments, on each of the three sampling days, at each of the two depths and for each of the three treatments.

Experiment	Sampling days	Depth (m)	Treatment (% loss from Day 0)			Predation by fish (%)
			Control	Partial cage	Full cage	
1	1 (21)	0–5	39 ^a	31 ^a	48 ^a	0
		5–10	57 ^a	0 ^a	42 ^a	15
	2 (43)	0–5	81 ^a	90 ^a	96 ^a	0
		5–10	85 ^a	92 ^a	63 ^a	22
	3 (64)	0–5	93 ^a	95 ^a	92 ^a	2
		5–10	93 ^a	96 ^a	89 ^a	4
2	1 (21)	0–5	27 ^b	0 ^{ab}	0 ^a	93
		5–10	0 ^b	0 ^{ab}	0 ^a	74
	2 (42)	0–5	0 ^b	10 ^{ab}	4 ^a	0
		5–10	75 ^b	36 ^{ab}	23 ^a	52
	3 (67)	0–5	51 ^b	50 ^{ab}	2 ^a	49
		5–10	74 ^b	39 ^{ab}	15 ^a	59
3	1 (20)	0–5	0 ^a	0 ^a	3 ^a	0
		5–10	0 ^a	7 ^a	0 ^a	16
	2 (41)	0–5	20 ^a	28 ^a	0 ^a	22
		5–10	0 ^a	0 ^a	22 ^a	0
	3 (63)	0–5	0 ^a	46 ^a	0 ^a	6
		5–10	45 ^a	14 ^a	0 ^a	56
4	1 (22)	0–5	16 ^a	26 ^a	18 ^a	0
		5–10	26 ^a	23 ^a	16 ^a	10
	2 (43)	0–5	31 ^a	27 ^a	23 ^a	8
		5–10	22 ^a	48 ^a	31 ^a	0
	3 (61)	0–5	28 ^a	40 ^a	30 ^a	0
		5–10	40 ^a	40 ^a	28 ^a	12

Note: Losses in the full cage treatment represent unexplained losses. Data are the raw relative changes calculated from raw mussel densities. Superscript letters represent the Tukey adjusted pairwise comparisons for differences among cage treatments on each sampling day and at each depth.

3.1.1 | Experiment 1 | Initial Seeding (Mussels 0.9 mm SL)

Pairwise differences show mussel density declined 36% (± 0.1 SE) between Days 0 and 21 ($g = 1.65$, $p < 0.01$) and a further 46% (± 0.1 SE) between Days 21 and 43 ($g = 1.32$, $p < 0.001$; i.e., $82\% \pm 0.1\%$ SE between days 0 and 43; $g = 2.99$, $p < 0.0001$). There was no difference in the relative change of mussel density between Days 43 and 64 ($g = 0.28$, $p = 0.73$). At the end of the experiment (64 days), the mean density of remaining spat averaged among treatments and depths was 3696 spat m^{-1} (± 4643 SE), which represented a 93.5% loss from the outset (i.e., 0 days; $g = 3.65$, $p < 0.0001$).

The mean density of dry mussock was different among treatments ($F_{(2,46)} = 3.59$, $p < 0.05$), sampling days ($F_{(3,45)} = 44.26$, $p < 0.0001$) and the interaction (sampling day $\times$ treatment $\times$ depth; $F_{(6,48)} = 3.57$, $p < 0.01$; Figure 5). Pairwise differences show there was 59.9% and 58.9% less dry mussock in the control

treatments than the full cages on Day 43 at the 5–10 m depth ($g = 1.43$, $p < 0.05$) and on Day 64 at the 0–5 m depth ($g = 1.12$, $p < 0.01$), respectively. No other pairwise differences were observed.

The mean density of dry algae was different among sampling days ($F_{(3,29)} = 7.50$, $p < 0.001$) but not treatments ($F_{(2,31)} = 1.76$, $p = 0.19$), depth ($F_{(1,33)} = 0.04$, $p = 0.85$) or any of the interaction terms (Figure 6). Pairwise differences show the dry weight of algae decreased between Days 0 and 43 ($g = 0.83$, $p < 0.05$), 21 and 43 ($g = 1.47$, $p < 0.05$), 0 and 64 ($g = 1.03$, $p < 0.05$) and Days 21 and 64 ($g = 1.72$, $p < 0.01$).

3.1.2 | Experiment 2 | Juveniles (Mussels 25 mm SL)

Pairwise differences show there was an overall difference in mussel density between the control treatments and the full cages

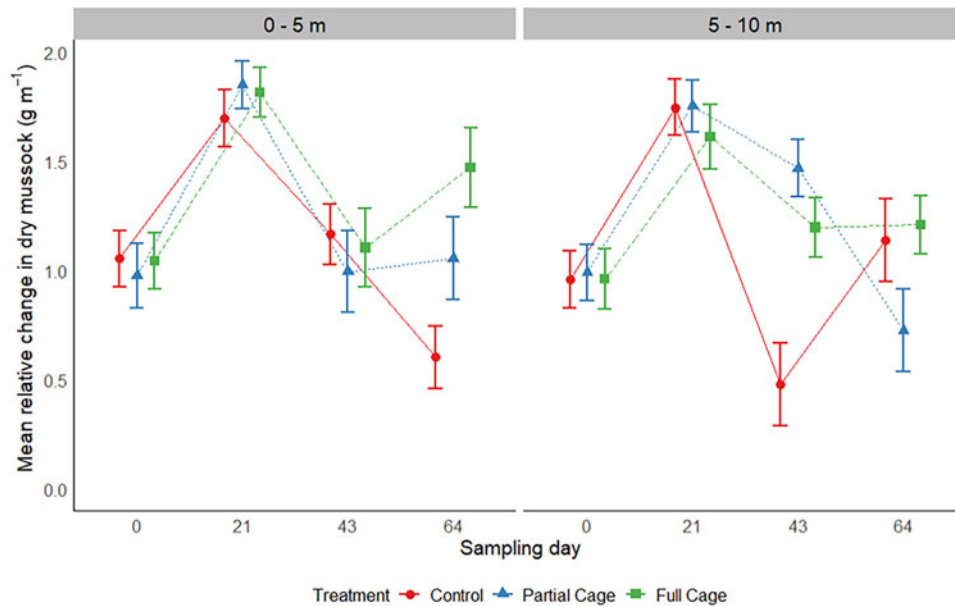


FIGURE 5 | Mean relative change of the dry weight ($\text{g m}^{-1} \pm \text{SE}$) of mussock on dropper lines for each of three fish predator caging treatments (i.e., control—no cage, partial cage and full cage) at each of two depths (0–5 and 5–10 m) for each of four sampling days in Experiment 1. Means are the derived means from the Lmer model. Error bars are jittered to prevent overlap.

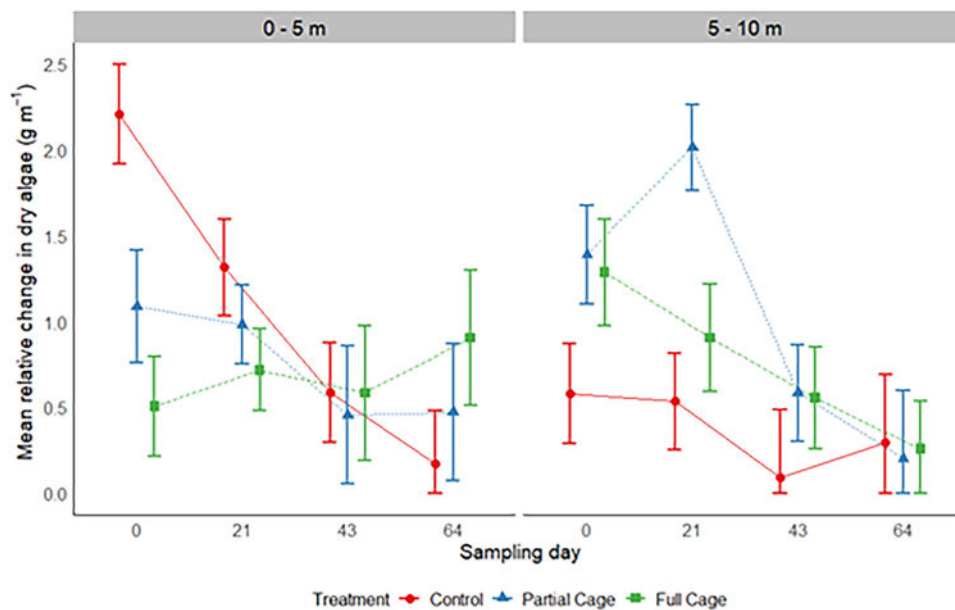


FIGURE 6 | Mean relative change of the dry weight ($\text{g m}^{-1} \pm \text{SE}$) of algae on dropper lines for each of three fish predator caging treatments (i.e., control—no cage, partial cage and full cage) at each of two depths (0–5 and 5–10 m) for each of four sampling days in Experiment 1. Means are the derived means from the Lmer model. Error bars are jittered to prevent overlap.

($g = 1.10$, $p < 0.001$) but not between any other treatment comparisons because the overall mean density of mussels in partial cages was intermediate between the two other treatments. Pairwise comparisons among sampling days identified the following paired days as different, with the latter day always having a decrease in mean mussel density; Days 0 and 67 ($g = 0.97$, $p < 0.01$), Days 21 and 42 ($g = 1.56$, $p < 0.0001$), Days 21 and 67 ($g = 1.87$, $p < 0.0001$).

At the end of the experiment (i.e., 67 days), the mean density of remaining mussels was $692 \text{ mussels m}^{-1}$ ($\pm 152 \text{ SE}$) in control treatments, $1080 \text{ mussels m}^{-1}$ ($\pm 106 \text{ SE}$) in partial cages and $1732 \text{ mussels m}^{-1}$ ($\pm 84 \text{ SE}$) in full cages.

Losses attributable to predation by fish ranged between 74% and 93% on Day 21, 0% and 52% on Day 42 and 49% and 59% on Day 67 (Table 4).

3.1.3 | Experiment 3 | Inter-Seed (Mussels 38 mm SL)

There were no differences in the density of mussels remaining attached to the dropper line at any level of the experiment. However, on the final sampling day (63 days), there was a trend toward higher mean densities in the full cage treatment at both depths; that is, density of mussels at the 0–5 m depth was 231 mussels m^{-1} (± 25 SE) in the control treatment, 118 mussels m^{-1} (± 24 SE) in partial cages and 244 mussels m^{-1} (± 26 SE) in full cages. At the 5–10 m depth, the density of mussels was 119 mussels m^{-1} (± 22 SE) in control treatment, 187 mussels m^{-1} (± 22 SE) in partial cages and 250 mussels m^{-1} (± 31 SE) in full cages.

3.1.4 | Experiment 4 | Final-Seeding (Mussels 44 mm SL)

Pairwise differences show mussel density declined 22% (± 0.05 SE) between Days 0 and 22 ($g = 1.75$, $p < 0.001$), and 30% (± 0.05 SE) between Days 0 and 43 ($g = 2.27$, $p < 0.0001$) but was not different between Days 22 and 43 ($g = 0.58$, $p = 0.18$). At the end of the experiment (61 days), mussel density had declined 33% (± 0.05 SE) from the initial density at Day 0 ($g = 2.52$, $p < 0.0001$). There was no difference in the relative change of mussel density between Days 43 and 61 ($g = 0.21$, $p = 0.85$). At the end of the experiment, the mean density of remaining mussels averaged among treatments and depths was 163 mussels m^{-1} (± 8 SE). The overall unexplained losses (i.e., losses in full cages) ranged between 18% and 16% on Day 22, 23% and 31% on Day 43 and 28% and 30% on Day 61.

Visual examination of the remaining mussock in the recovered samples, especially those recovered 22 days after deployment (0 days), indicated differences in the integrity of the mussock related to treatment. The mussock in full cages was mostly fully intact and remaining in position, whereas in the control samples, and to a lesser extent for the partial cages, there were tears in the mussock with the underlying mussels or dropper line exposed.

The mean dry weight of mussock remaining attached to the dropper lines differed among sampling days ($F_{(3, 29)} = 70.57$, $p < 0.0001$), treatments ($F_{(2, 28)} = 3.95$, $p < 0.05$) and their interaction ($F_{(6, 27)} = 4.97$, $p < 0.01$) but not between depths or any other interaction terms (Figure 7).

At the beginning of the experiment, the mean dry weight of mussock on the dropper lines was 15.3 g m^{-1} (± 0.8 SE). Pairwise comparisons show after 22 days the mean dry weight of mussock in control samples was 51% (± 0.17 SE) less than for full cages ($g = 2.11$, $p < 0.0001$) and 65% (± 0.17 SE) less than for the partial cages ($g = 1.14$, $p < 0.01$). There was no difference in the mean dry weight of mussock between the full and partial cages. After 43 days, the mussock had fully degraded in all treatments, and subsequently, at the end of the experiment (i.e., 61 days), there was no mussock left on any treatments.

3.2 | Mussel Growth

The mean SL of mussels remaining on the dropper line was different for the interaction (sampling day $\times$ treatment $\times$ depth)

in Experiment 1 ($F_{(6, 6070)} = 16.92$, $p < 0.0001$), Experiment 2 ($F_{(6, 88,137)} = 329.33$, $p < 0.001$), Experiment 3 ($F_{(6, 22,864)} = 36.18$, $p < 0.001$) and Experiment 4 ($F_{(6, 17,625)} = 41.8$, $p < 0.001$; Figure 8). At the beginning of the experiments, the overall mean SL of mussels was 0.93 mm (± 0.013 SE) in Experiment 1, 24.5 mm (± 0.03 SE) in Experiment 2, 38.0 mm (± 0.2 SE) in Experiment 3 and 43.5 mm (± 0.09 SE) in Experiment 4.

Mussel size increased gradually across all of the experiments with mussels in full cages tending toward larger sizes at the end of all four experiments (Table 5).

There were differences in the size distribution of mussels among the three treatments at the two depths at the end of Experiment 1 ($\chi^2 = 696.21$, $p < 0.0001$; Figure 9A), Experiment 2 ($\chi^2 = 460.84$, $p < 0.0001$; Figure 9B), Experiment 3 ($\chi^2 = 424.44$, $p < 0.0001$; Figure 9C) and Experiment 4 ($\chi^2 = 628.6$, $p < 0.0001$; Figure 9D).

At the 0–5 m depth, control samples were consistently skewed toward smaller mussels, lacking larger size classes. Partial cages showed no consistent trend, with size bias alternating between small and large mussels among experiments. Full cages showed a general tendency toward more large mussels but not in every case.

At the 5–10 m depth, controls were typically skewed toward smaller size classes, but the specific size categories that increased or decreased differed among experiments. Partial cages did not exhibit a consistent directional shift in size distribution. Full cages were consistently weighted toward larger size classes with a universal reduction in smaller mussels among all experiments.

4 | Discussion

4.1 | Mussel Losses

The experimental caging of initial seeding (0.9–8 mm SL, Experiment 1), juvenile (25–34 mm SL, Experiment 2), inter-seed (38–49 mm SL, Experiment 3) and final-re-seeded (44–54 mm SL, Experiment 4) Greenshell mussels each for a period of 2 months recorded significant mussel losses. Observed losses were up to 93% for mussels of 0.9–8 mm SL, up to 75% for mussels between 25 and 34 mm SL, 45% for mussels between 38 and 49 mm SL and up to 40% for mussels between 44 and 54 mm SL. Despite this, there was only statistical evidence of significant losses of mussels due to predation by fish in one of the four experiments, contrary to anecdotal reports from the mussel farmers that large losses of mussels consistently occur shortly after seeding or re-seeding of mussels onto farms. Although there were visual indications of possible fish predation on the control and partial cage treatments, there was only a statistically confirmed difference in the density of mussels among experimental treatments in Experiment 2 for juvenile mussels (25–34 mm SL). Losses attributable to fish predation in this experiment were estimated by the model to be 38%, but the observed losses ranged from 0% to 93%, indicating that for the experimental caging method to reliably detect predation effects, mean mussel losses would need to exceed 30%. In contrast, losses observed in the full cage treatments, presumed to reflect non-predatory losses, ranged from 0% to 23%. This suggests that, for mussels of this size class, fish predation is likely a more

TABLE 5 | Summary of the mean shell length (SL) and percentage of growth from Day 0 of mussels sampled in each of the four experiments, on each of the three sampling days after Day 0, at each of the two depths.

Experiment	Sampling day	Depth (m)	Mean mussel SL (mm ± SE)			Mean growth (% from Day 0)		
			Control	Partial cage	Full cage	Control	Partial cage	Full cage
1	1 (21)	0–5	1.33 (±0.04) ^a	1.45 (±0.05) ^{ab}	1.59 (±0.06) ^b	42	55	70
		5–10	1.61 (±0.06) ^a	1.63 (±0.05) ^a	2.63 (±0.11) ^b	72	75	182
	2 (43)	0–5	3.41 (±0.08) ^a	4.28 (±0.08) ^b	4.44 (±0.08) ^b	265	358	375
		5–10	4.01 (±0.07) ^a	4.29 (±0.07) ^b	4.86 (±0.08) ^c	329	359	420
	3 (64)	0–5	6.16 (±0.09) ^a	6.64 (±0.10) ^b	8.42 (±0.12) ^c	560	611	802
		5–10	4.58 (±0.08) ^a	6.33 (±0.11) ^b	7.49 (±0.10) ^c	390	578	702
2	1 (21)	0–5	23.84 (±0.07) ^b	29.44 (±0.07) ^c	26.95 (±0.07) ^a	0	20	10
		5–10	27.47 (±0.06) ^b	24.88 (±0.05) ^a	24.76 (±0.07) ^a	12	2	1
	2 (42)	0–5	31.75 (±0.09) ^b	32.58 (±0.13) ^c	30.79 (±0.11) ^a	26	33	26
		5–10	32.47 (±0.13) ^b	30.63 (±0.14) ^c	26.75 (±0.19) ^a	33	25	9
	3 (67)	0–5	31.55 (±0.16) ^b	35.15 (±0.13) ^c	32.95 (±0.23) ^a	29	44	35
		5–10	34.42 (±0.15) ^b	34.81 (±0.13) ^{ab}	35.09 (±0.13) ^a	41	42	43
3	1 (20)	0–5	39.66 (±0.26) ^a	45.18 (±0.91) ^b	39.62 (±0.39) ^a	4	19	4
		5–10	39.47 (±0.38) ^{ab}	40.89 (±0.40) ^b	39.27 (±0.37) ^a	4	8	3
	2 (41)	0–5	41.51 (±0.50) ^b	41.96 (±0.52) ^b	46.10 (±0.43) ^a	9	10	21
		5–10	40.19 (±0.42) ^b	46.60 (±0.35) ^c	44.02 (±0.48) ^a	6	23	16
	3 (63)	0–5	47.65 (±0.36) ^b	47.17 (±0.60) ^b	53.54 (±0.35) ^a	25	24	41
		5–10	46.83 (±0.52) ^a	46.88 (±0.50) ^a	48.42 (±0.49) ^a	23	23	27
4	1 (22)	0–5	41.85 (±0.23) ^b	42.20 (±0.35) ^b	39.94 (±0.25) ^a	0	0	0
		5–10	43.99 (±0.25) ^b	44.47 (±0.24) ^b	39.35 (±0.31) ^a	1	2	0
	2 (43)	0–5	47.41 (±0.20) ^a	49.20 (±0.21) ^b	48.70 (±0.24) ^a	9	13	12
		5–10	50.73 (±0.22) ^b	50.56 (±0.36) ^b	52.69 (±0.24) ^a	17	16	21
	3 (61)	0–5	51.82 (±0.25) ^b	57.20 (±0.47) ^c	54.44 (±0.24) ^a	19	32	25
		5–10	52.23 (±0.21) ^b	49.97 (±0.26) ^c	56.40 (±0.24) ^a	20	15	30

Note: Superscript letters represent the Tukey adjusted pairwise comparisons for the treatment $\times$ depth $\times$ sampling days interaction.

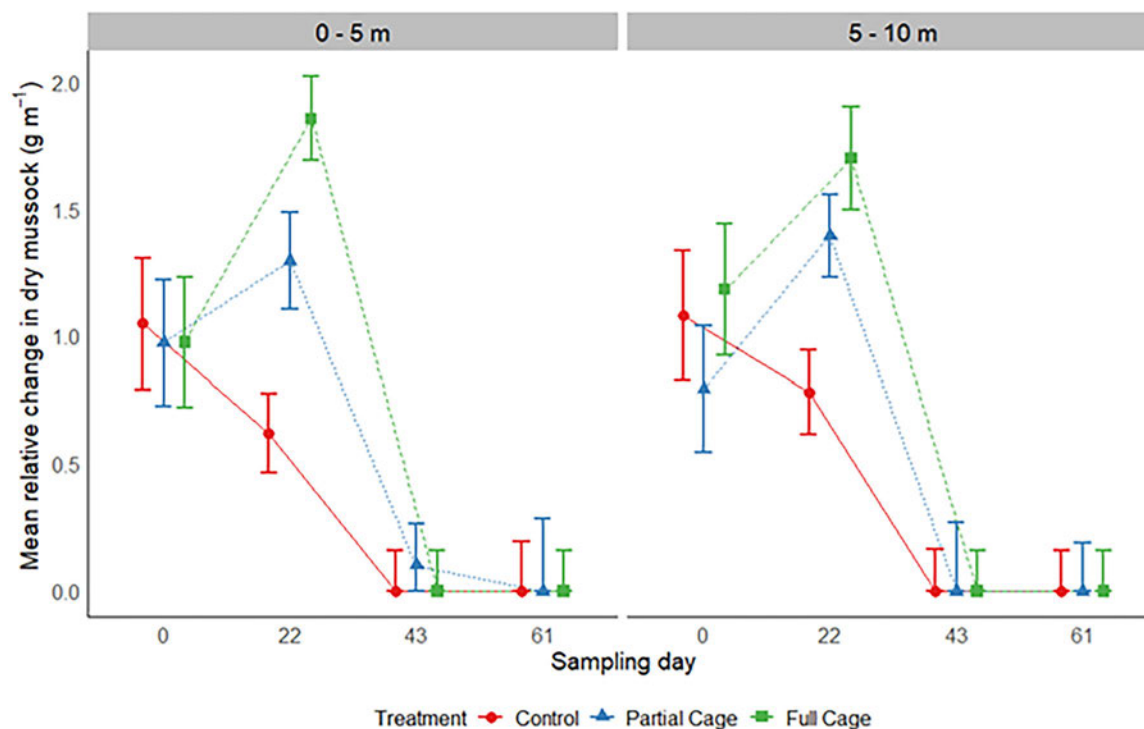


FIGURE 7 | Mean relative change of the dry weight ($\text{g m}^{-1} \pm \text{SE}$) of mussock on dropper lines for each of three fish predator caging treatments (i.e., control—no cage, partial cage and full cage) at each of two depths (0–5 and 5–10 m) for each of four sampling days in Experiment 4. Means are the derived means from the Lmer model. Error bars are jittered to prevent overlap.

substantial cause of losses than other unmeasured factors such as handling stress, dislodgement or environmental conditions (Hayden and Woods 2011; South et al. 2022).

The overall extent of mussel losses was markedly different between the two smaller size classes of mussels examined in this study. In Experiment 1 (i.e., mussels 0.9–8 mm SL), losses of up to 96% of mussels were recorded in all treatments, including the full cages, over 64 days. However, despite the magnitude of these losses, the caging experiment did not provide conclusive evidence that predation by fish made a significant contribution, although it may have been a contributing factor (i.e., between 0% and 22%). This is consistent with previous research on mussels of this size which shows that mussel losses on Greenshell farms often exceed 90% in the first few months of production, reaching as high as 99%, which is thought to be related to a variety of causes, but especially the innate secondary migration behaviour of spat of small size in this mussel species (Skelton and Jeffs 2021; South et al. 2022). There were some observations of torn mussock in control samples in Experiment 1, consistent with RUV observations of parore attacking the spat lines (mussels 0.9–8 mm SL) at this same study site (Stobart, Jeffs, Hillman, et al. 2025; Figure 10). Likewise, there was up to 60% less dry mussock measured in the control treatments than the full cages during Experiment 1 consistent with damage by fish. It was hypothesised that parore may have contributed to losses of mussels by targeting spat-encrusted macroalgae. However, given the extremely high losses of mussels in Experiment 1, it seems unlikely that parore would be unlikely to be a major contributor to the overall losses of spat in this experiment. Therefore, although some fish predation likely occurred (up to 20%), the relative contribution of predation

to mussel losses at this early production stage is low compared to other factors, such as secondary migration of mussel spat (Skelton and Jeffs 2021).

The results from Experiment 2 suggest that predation did not occur steadily but rather sporadically over the 67 days. For example, the observed losses ranged between 74%–93% on Day 21, 0%–52% on Day 42 and 49%–59% on Day 67. This indicates that predation events may be episodic, occurring intensely at certain times while being less intense or absent at others. This observation aligns with anecdotal reports from mussel farmers in this area, who report that predation can happen sporadically or all at once, often leading to substantial losses within a short period (M. Moy, Aroma (NZ) Ltd., New Zealand, pers. comm.). Farmers have reported seeding their dropper lines only to find them completely stripped of mussels a few days later. While sampling for Experiment 2, Australasian snapper were observed in large schools and RUV deployments captured these schools engaged in feeding activities on the mussel dropper lines (Stobart, Jeffs, Hillman, et al. 2025; Figure 11). Therefore, it is likely that snapper were responsible for the losses of up to 93% of the mussels between 25 and 34 mm SL over the course of this experiment.

Experiments 1 and 4 were both characterised by high variability in the measured mussel density at all levels of the experiments, among treatments, depths and all sampling days. This high variability may have prevented the detection of mussel losses due to fish predation for these experiments. Given the variability of seeding density and the sporadic nature of fish predation, increasing replication to at least two to three times that of the

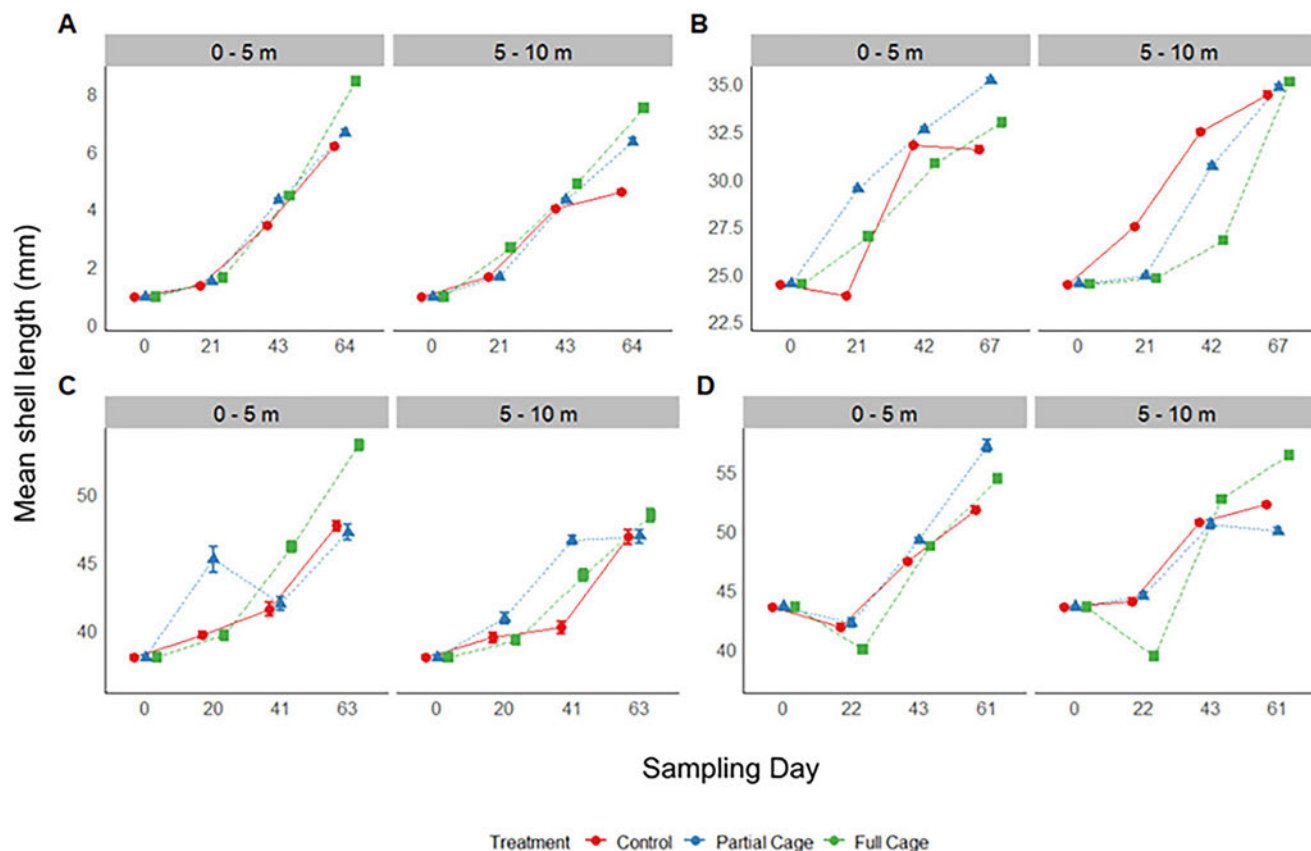


FIGURE 8 | Mean SL of mussels (mm $\pm$ SE) on dropper lines for each of three fish predator caging treatments (i.e., control—no cage, partial cage and full cage) at each of two depths (0–5 and 5–10 m) for each of the four sampling days in (A) Experiment 1, (B) Experiment 2, (C) Experiment 3 and (D) Experiment 4. Means are the raw means. Error bars are jittered to prevent overlap.

current study and extending the duration of the experiment by at least 3 weeks may provide a greater ability to detect fish predation of smaller extent than was possible in this current study. This should be undertaken concurrently with continuous RUV deployments which could help to determine the timing of predation events and the species of fish responsible.

The size of mussels confirmed to be predated by fish in this current study is inconsistent with the results of studies in European mussel-farming regions, which have confirmed fish predation of 54%–90% of farmed *M. galloprovincialis* to occur at sizes between 34 and 54 mm SL (Richard et al. 2020; Šegvić-Bubić et al. 2011). In both European studies, experimental monitoring of mussel losses began immediately after re-seeding, prior to the formation of secure byssal attachments. The rapid and substantial losses of mussels that were observed during this period may partly reflect fish being attracted to the area by the disturbance and activity associated with re-seeding operations. This would align with underwater video observations of fish activity around mussel farms in the Firth of Thames where Australasian snapper abundance was higher during the process of lifting and lowering mussel farm lines in the water compared to hours later after the farming activity had ceased (Stobart, Jeffs, Hillman, et al. 2025). Likewise, both European studies found that the high losses of mussels were associated with observations of large aggregations of gilthead seabream (*S. aurata*). The losses of mussels estimated in these studies are substantially higher than those measured in

similar size classes in the present study; however, without using exclusion experiments to validate the observed losses in such studies, the losses of mussels attributed to predation by fish may also include mussel losses caused by dislodgement, migration and mortality of the newly seeded mussels (Capelle, Wijsman, et al. 2016). To this effect, in Experiment 4 (43–54 mm SL) of the present study, there was an overall decline in mussel density after 2 months of around 33%, regardless of the caging treatment. Observed losses to fish predation ranged between 0% and 12% over the duration of the experiment; however, the absence of an effect from experimental caging on mussel density would suggest that the observed losses of final-re-seeded mussels are due to other factors, such as dislodgement or natural mortality following re-seeding (Capelle, Wijsman, et al. 2016). Therefore, attributing losses of farmed mussels to any single factor, such as fish predation, without direct evidence is imprudent because losses of mussels from production appear likely to be due to multiple causes.

Historically, predation by fish of up to 100% has also been recorded in the farming of oysters (Brown et al. 2003, 2008; Richard et al. 2020; Saito et al. 2008), clams (Feldman et al. 2004; Goodwin and Pease 1989; Hart et al. 1998, 1999; Heslinga et al. 1984) and scallops (Hortle and Cropp 1987; O'Connor et al. 1999; Strand 2004; Strohmeier et al. 2006). Despite this, the adoption of farming clams and scallops in enclosed structures, such as pearl or lantern nets in the case of scallops and plastic

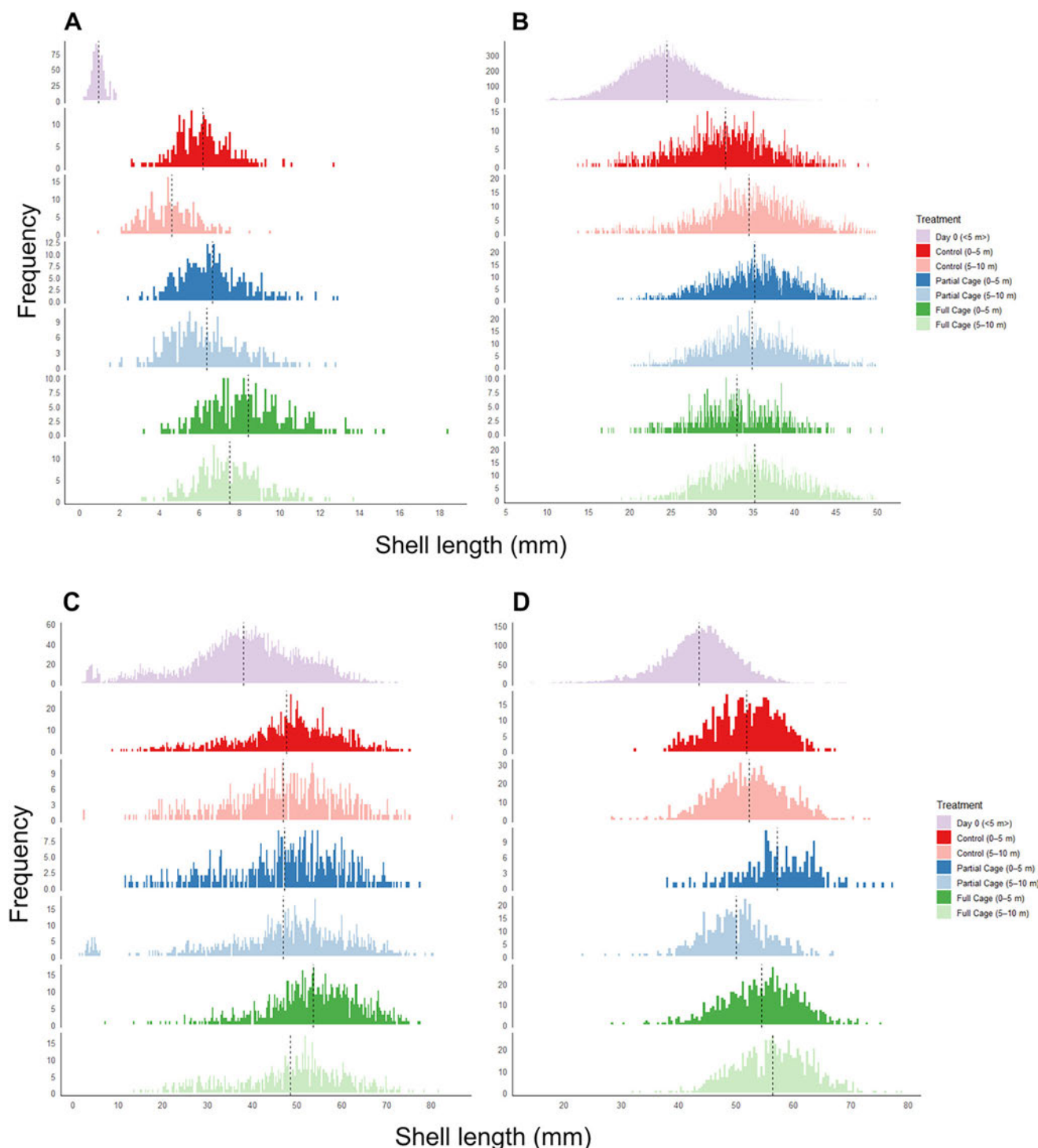


FIGURE 9 | Frequency of mussels by SL (mm) at the initial sampling day (Day 0) for all treatments and depths, and at the final sampling day (A: Day 64 and B: Day 67) for each of the three treatments, at each of the two depths (0–5 and 5–10 m) in (A) Experiment 1, (B) Experiment 2, (C) Experiment 3 and (D) Experiment 4. Dashed black lines indicate the mean SL for each treatment group.

mesh bags, metal cages or plastic tubes in the case of clams, has significantly mitigated the issue (Bendell 2015; Cahill et al. 2023; Heslinga et al. 1984; Munroe et al. 2015; Pearce et al. 2019). Losses of oysters remain comparable to mussels when farmed in suspended or bottom culture without exclusion measures; however, their susceptibility to predation is significantly reduced when housed in trays, nets, cages or mesh bags (Stobart, Jeffs, Skelton 2025). This suggests that excluding fish from shellfish

farming structures has been highly effective at limiting fish predation in other shellfish farming industries.

4.2 | Growth

Selective predation of larger mussels by fish may have resulted in the mean size of mussels overall being smaller in the control



FIGURE 10 | Photograph of parore (*Girella tricuspidata*) feeding on recently seeded spat lines in Experiment 1 at the Hautapu spat site (Stobart, Jeffs, Hillman, et al. 2025).



FIGURE 11 | Photograph of Australasian snapper (*Chrysophrys auratus*) feeding on juvenile mussel lines in Experiment 2 at the Esk Point site (Stobart, Jeffs, Hillman, et al. 2025).

and partial cage treatments than in the cages in this study. For instance, previous research found the mean size of mussel spat in full cages grew to be larger than in control and partial cage treatments and this was attributed to larger mussels being preferentially consumed by fish (Hayden 1995). However, fish predation was not detected in Experiments 1, 3 and 4. Therefore, these differences in growth of caged mussels are more likely the result of reduced predator defence mechanisms for mussels in cage treatments. For example, it has been found that blue mussels (*M. edulis*) raised in the absence of predatory whelks and crabs grew to larger sizes with thinner shells than those exposed to predators in a hatchery experiment (Smith and Jennings 2000). Changes in growth may reflect resource allocation differences in response to predators likely as a result of feeding reductions

whereby in the presence of predators, the mussels react by closing their valves (Robson et al. 2010).

The size of mussels predated by fish likely varies by fish species and size. The fish families known to feed on mussel farms include sparids, girellids, monacanthids and labrids (Hayden 1995; Peteiro et al. 2010; Richard et al. 2020; Šegvić-Bubić et al. 2011; Stobart, Jeffs, Hillman, et al. 2025). There is evidence that, although girellid fishes are omnivorous, their jaw morphology is primarily adapted for grazing and scraping rather than crushing hard-shelled prey, potentially limiting their ability to consume mussels beyond early juvenile stages (Salewski 2017). In contrast, sparids and wrasses are well adapted for consuming hard-bodied prey, such as mussels, and have been shown to consume mussels

of all sizes, with larger fish able to consume larger mussels (Hayden 1995; Underwood et al. 2024; Usmar 2012). Therefore, the vulnerability of mussels would change within and between farming regions based on the composition of fish assemblages.

It is possible that some mussel size refuge exists whereby fish are less likely to target mussel lines where the mussels are smaller than 1 mm or greater than 38 mm. For instance, toward the end of Experiment 1, when mussels grew to a size that they were visible to the naked eye (i.e., 6–8 mm SL), there was a trend for the full cage treatments to have a higher density of mussels than control treatments, possibly as a result of predation by fish beginning to occur as the size of the mussels increased. This is consistent with previous research which found full cage predator exclusion to significantly reduce losses of Greenshell mussels between 9 and 15 mm SL by up to 100% (Hayden 1995). Unfortunately, during the period of this study, it was not possible to undertake a caging experiment for mussels of size 10–20 mm SL which would have helped to have confirmed the existence of fish predation of farmed mussels in this size range.

4.3 | Implications for Aquaculture Management

Spat losses in the initial seeding stage (<1 mm SL) of mussel production frequently exceed 90% and often reach up to 99% (Skelton and Jeffs 2021). Under such high baseline mortality, even marginal gains in spat retention can result in substantial improvements in production. For instance, a 1% increase in survival at seeding would effectively double the number of individuals advancing to later stages of production. If predation by fish contributes even a small proportion of early-stage loss, mitigating this impact could yield meaningful gains in production. In this study, average seeding density at the outset of Experiment 1 was 57,205 spat per metre of dropper line. If a single 5–10 cm section was dislodged through predation by fish, this would equate to the loss of 2860–5731 spat, equivalent to 77%–155% of the total spat density recorded at Day 64 (3696 spat m⁻¹). Although these events may not be statistically detected due to high background variability, the production implications are considerable.

Despite this, fish predation remains a less significant contributor to the loss of mussels at this early seeding stage. Extensive research shows that the size (0.5–3 mm SL) and density (~17,640 spat m⁻¹) at which mussels are seeded in New Zealand is extremely inefficient due to the multitude of sources for spat loss (Skelton and Jeffs 2021, 2022; Skelton et al. 2022; South et al. 2022). Secondary settlement is a leading cause of losses of early-stage mussels with spat able to continue secondary migration up to 24 mm SL (Skelton et al. 2021; Ram et al. 2026). In other parts of the world, mussels are seeded at larger sizes by accessing sources of larger juveniles or through the use of a nursery culture stage which allows the mussels to reach a size beyond their ability to undergo secondary migration. Therefore, the most practical first step would be to develop a nursery culture stage of production for Greenshell mussels in New Zealand (Skelton et al. 2021).

Following nursery culture, mussels could be seeded onto farms within areas of fish exclusion by means of physical barriers or deterrent systems (Stobart, Jeffs, Skelton 2025). Exclusion could be used until mussels have attached themselves to the grow-

out rope and they exceed 35 mm SL where the results of this study indicate that losses of mussels decline markedly. However, recent research shows that even at larger sizes, fish will tear open mussock and consume mussels of larger sizes (60 mm SL; Mason et al. 2026); hence, exclusion is necessary until the mussels are securely attached to the grow rope. This would maintain habitat value, such as recruitment and trophic enhancement within farm habitats (Stobart, Jeffs, Hillman, et al. 2025; Underwood et al. 2023), while reducing mussel losses during early-stage production. Adopting this approach would support both production goals and conservation outcomes, enabling fish to benefit from the shelter and food provided by farm habitats, while also contributing to surrounding fisheries and recreational value (Gibbs 2004).

4.4 | Limitations and Future Directions

In this study, the detection of fish predation through exclusion experiments depended on two key conditions: low background losses of mussels due to causes other than predation and predation losses exceeding approximately 30%. At the initial seeding stage, background losses of mussels were high, precluding the statistical determination of the contribution of fish predation to the overall losses. The inability to detect an effect under these conditions does not imply that predation is negligible. Rather, it reflects a methodological limitation common in high-mortality scenarios where the signal of predation is obscured by high background signal.

Small-scale caging may be ineffective at detecting the true magnitude of fish predation, particularly when it varies significantly across spatial and temporal scales (Englund et al. 1996). Previous studies have shown inconsistent temporal effects of fish predation across different mussel aquaculture sites (e.g., Hayden 1995; Šegvić-Bubić et al. 2011). Additionally, the quality of nearby habitat can impact fish presence, with areas of higher fish abundance typically experiencing greater predation (Hindell et al. 2001). Consequently, small-scale caging experiments may fail to reflect the true magnitude of predation due to artefacts, site-specific variables, and the spatial and temporal variability of predation (Barros 2005). Additionally, although physical exclusion methods can reduce predation in the short term, their long-term use introduces operational and ecological complications. Structures intended to exclude fish also provide settlement surfaces for biofouling organisms, which would ultimately result in increased maintenance costs and reduced farm efficiency (Stobart, Jeffs, Skelton 2025). The accumulation of biofouling communities may also affect the availability of nutrients, impacting the growth and production of mussels (Sievers et al. 2013).

Where experimental resolution is limited, inferences must be made on converging indicators rather than on confirmation of a single line of evidence or the convergence of partially independent streams of evidence (Linkov et al. 2006). For example, in terrestrial agriculture, thresholds of action for pest management can be set based on expected damage functions and vulnerability windows, not on conclusive evidence of crop consumption by pests (Tang et al. 2010). In salmon aquaculture, predation by seals is inferred from behavioural data and proximity rather than direct ingestion (Quick et al. 2004). Thus, the amount of evidence

needed for explanatory closure may be greater than that needed for intervention.

On-farm research of the nature presented in this study is highly reliant on the production programme of industry research partners, resulting in experiments being conducted at sites where mussels are available at specific times, which may not coincide with the locations or timing of fish presence or feeding activity that results in mussel predation. A much more extensive study would be required to determine the spatial and temporal variability of fish predation from mussel farms. It is unlikely that such a study could use the caging methods deployed in this current study, given the considerable resources required. Instead, an alternative experimental approach would need to be developed, such as continuously monitoring entire dropper lines and recording sections that are clearly stripped by fish (Figure 5), alongside deploying multiple remote underwater camera systems to monitor fish predation activity. This method has the potential to be more effective at capturing large-scale fish predation events while not also capturing the losses of mussels due to other causes such as dislodgement or natural mortality.

5 | Conclusions

Overall, the results from this study indicate that fish predation is sporadic but can be an important contributor to the loss of mussels on Greenshell mussel farms in the Firth of Thames in north-eastern New Zealand, with losses reaching up to 93% in mussels between 25 and 34 mm SL over a period of 67 days. Despite consistent observations of torn mussock, damaged line and broken shells in predator-exposed treatments, the small-scale experimental caging method used in this study was ineffective at isolating fish predation from other causes of mussel losses in the <8 mm SL and >38 mm SL size classes where losses of mussels reached 94% and 35% after 2 months, respectively. Therefore, the development of fish predation mitigation strategies at initial seeding (<1 mm SL), inter-seeding (>38 mm SL) and final-re-seeding (>44 mm SL) stages of production are unlikely to improve production output substantially without first identifying and addressing other causes of mussel losses, which this study indicates are substantial. Mussels in caged treatments in the current study generally grew faster than uncaged mussels, suggesting that protection from predators could be useful for enhancing the growth of mussels.

Predation of cultured mussels by fish is likely to begin somewhere in the 8–25 mm SL size range; however, additional experiments would be required to investigate fish predation in this size range not covered by this current study. Future research should also aim to improve the efficiency of the methods for measuring the extent of fish predation of mussels in aquaculture, perhaps by combining a range of detection methods, such as direct RUV observations of fish activities in conjunction with non-destructive assessment of changes in mussel abundance on dropper lines.

Author Contributions

Rebecca L. Stobart: conceptualisation, methodology, software, formal analysis, investigation, data curation, writing – review and editing, writing – original draft, visualisation, project administration. **Andrew G. Jeffs:**

conceptualisation, methodology, validation, writing – review and editing, supervision, resources, funding acquisition. **Jenny R. Hillman:** validation, writing – review and editing, supervision. **Bradley M. Skelton:** conceptualisation, resources, writing – review and editing, supervision, project administration, funding acquisition.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available upon reasonable request.

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