Evaluation of the potential for anti-predator stocking to reduce crop losses due to fish predation in Greenshell™ mussel (*Perna canaliculus*) farms

Thomas Cary Mason[1*], Andrew G. Jeffs[1,2], and Bradley M. Skelton[1]

[1] Institute of Marine Science, University of Auckland, Private Bag 92019, Auckland, New Zealand

[2] School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

*Corresponding author: Orcid ID; 0009-0004-3664-5414

Abstract

Enormous losses of juvenile mussels are commonplace in mussel aquaculture worldwide. Fish predation is one important contributor to these losses in many mussel growing regions. The Greenshell™ mussel industry in New Zealand is particularly susceptible to fish predation, where farmers have reported losses of seed mussels of up to 100%. The current practice for seeding juvenile Greenshell™ mussels onto coastal farms is to deploy the mussels alongside a continuous longline growing rope enclosed in a cotton stocking which holds the mussels against the rope. The mussels subsequently attach to the rope with byssus threads before the cotton degrades. During this vulnerable period, the stocking may also help to protect the juvenile mussels from fish predators whilst they are unattached to any substrate. This study investigated whether differences in the strength and weave of three types of stocking (i.e., a 54-loop weave commonly used in New Zealand, a smaller and more tightly woven stocking used in shellfish hatcheries, and a 42-loop stocking that combines two weaves of cotton together) might affect the amount of fish predation on juvenile mussels that were newly seeded onto growing rope. In an experiment, the three types of cotton stocking were each subjected to three levels of predation by restricting fish access to the growing ropes seeded with juvenile mussels by attaching full, partial and no plastic mesh cages around the ropes. The number of mussels lost from each of the treatment combinations were assessed after 12, 31, and 45 days. At 45 days on average only 15.1% (± 1.7 SE) of the seeded juvenile mussels remained on those growing ropes subjected to full fish predation, with no differences in mussel losses among three types of socking. In contrast, on average 90.7% (± 2.1 SE) of the seeded juvenile mussels remained on growing ropes protected from fish predation by the full mesh cages, and 87.5% (± 3.7 SE) for partial cages. For both types of protective cages there was no difference in the numbers of remaining juvenile mussels among the three types of stocking. Remote underwater video camera observations confirmed Australasian snapper (*Chrysophrys auratus*) were feeding on the juvenile mussels from the dropper ropes without protective cages. These results show that physical protection by cages protects juvenile mussels from fish predation, while cotton stocking, regardless of the type of stocking, is not effective for preventing fish predation. The results also show that the majority of mussel losses in the uncaged treatment occurred in the first 12 days of the experiment, indicating that vulnerability to predation may be associated with the initial lack of byssus attachment to the growing rope. Overall, these results point to a need to develop more effective methods for mitigating the high losses of seed mussels after they are seeded onto growing ropes.

Key words: Mussels, aquaculture, fish, predation, mitigation, deterrence

1. Introduction

Shellfish aquaculture is a major contributor to global aquaculture, accounting for 20% of global aquatic animal production in 2020, valued at nearly $30 billion USD (FAO 2024). Bivalves, primarily mussels, scallops, clams, and oysters, form the majority of this production, accounting for approximately 80% of total global molluscan shellfish aquaculture production. However, despite the success of these industries, bivalve production, particularly mussel production, is often characterized by substantial losses of juveniles, resulting in significant inefficiency. These losses are often caused by a variety of biotic and abiotic factors, including stresses associated with the harvest, transportation and seeding of seed, suboptimal environmental conditions at the time of seeding, and natural secondary settlement behaviour (South et al., 2020; South et al., 2021; Dégremont et al., 2007; Green-Gavrielidis et al., 2018; Skelton and Jeffs 2020). However, a major contributor to production losses, especially for mussel aquaculture, is predation by fish, which occurs throughout the world (Meira et al., 2024; Robert and Gérard, 1999; Underwood et al., 2023; Suplicy, 2017). For example, significant crop losses of up to 54% of newly-seeded juvenile Mediterranean mussels (*Mytilus galloprovincialis*) from farms in Croatia (Šegvić-Bubić et al., 2011), up to 80% loss of seed Mediterranean mussels in Slovenia (Ramšak et al., 2024), 68% loss of reseeded juveniles on mussel farms in southern France (Richard et al., 2020; Gervasoni and Giffon, 2016), 58% loss of recent mussel settlers on collector ropes deployed in northern Spain (Peteiro et al., 2010), and up to 100% loss of spat on Greenshell™ mussel (*Perna canaliculus*) farms in New Zealand (Hayden, 1995). More recently, persistent and increasing losses due to fish predation are thought to have contributed to stagnation and even decline in mussel aquaculture production in some regions of the Mediterranean Sea (Avdelas et al., 2021; FAO, 2024; Ramšak et al., 2024).

While fish predation in mussel aquaculture is a global issue, there is relatively little published research that has quantified the exact magnitude of losses either in product or financial terms. Even fewer publications have reliably determined the predatory species responsible, or sought to develop effective, practical, and cost-effective farm-scale methods of mitigation. Nonetheless, a wide range of methods for deterring fish from accessing a particular area or location have been tested across a broad range of applications and environments. For instance, physical and non-physical deterrents, such as netting barriers, underwater acoustic devices, bubble curtains, strobe lights, pheromones, and carbon dioxide have been used in a variety of situations such as preventing invasive fish from expanding their range within waterways and preventing them from entering hydroelectric and other industrial infrastructure (Maes et al., 2004; Noatch and Suski, 2012; Michaud and Taft, 2000). While such deterrents have been tested in both fresh- and brackish water, there is minimal research examining methods of deterring fish within open water marine environments, such as those in which mussel aquaculture is generally located (Cupp et al., 2021; Maes et al., 2004; Michaud and Taft, 2000; Noatch and Suski, 2012; Bullen and Carlson, 2003).

Of all the approaches used to deter fish, physical exclusion has often been found to be the most effective and simple method for preventing fish from accessing areas of interest, whether intentionally for invasive species population control (Michaud and Taft, 2000), or unintentionally when blocking migration routes or fragmenting populations (Branco et al., 2017; Cooke at al., 2022). However, its overall effectiveness varies depending on the specific application. For example, nets can be used to exclude fish from discrete areas in open waters, such as aquaculture areas, however, this is much more difficult in exposed waters where there is potential for storms or turbulent water to move or destroy netting (Munroe et al., 2015; Thomas, 2009; Belle and Nash, 2008; Anderson et al., 2015).

Most research on physical exclusion methods to limit fish predation on mussel farms has focused on farm-wide exclusion, which has been shown to be highly effective with other farmed bivalves as well as with mussels (George et al., 2008). For example, the deployment of nets to fully exclude fish from mussel farms resulted in increased yields of up to 60% on mussel farms in both Spain and France

(Peteiro et al., 2010; Richard et al., 2020). However, farm-wide physical exclusion may not always eliminate crop losses due to fish predation, as seen in France where surveys of bivalve farmers using recommended net enclosures still estimated crop losses due to fish of around 26% (Gervasoni and Giffon, 2016). The nets used to fully exclude fish from farming areas often require extensive maintenance and can sink, stretch, tear, and deteriorate over time reducing their effectiveness, and allowing fish to enter (Richard et al., 2020). Therefore, physical exclusion methods that protect the mussels themselves and require less maintenance may present a more viable and cost-effective approach for mitigating fish predation on mussel farms.

Physical exclusion of fish predators has potential to assist the Greenshell™ mussel aquaculture industry in New Zealand, which appears to be particularly susceptible to high losses of mussels due to fish predation. The Greenshell™ industry is among the most inefficient mussel aquaculture industries in the world, with crop losses in the early stages of production reported to frequently exceed 99% (Hayden, 1995; Skelton et al., 2022; South et al., 2020). A significant proportion of these losses is thought to be caused by fish predation, particularly on farms located throughout the North Island, where the Australasian snapper (*Chrysophrys auratus*, hereafter snapper) is thought to be responsible (Stobart et al., 2024). Reports from farmers suggest that predation by snapper can cause the complete loss of mussel crop from farms, often stripping seeded dropper ropes bare of any mussels in the process. Furthermore, anecdotal reports from farmers suggest that the problem is becoming more severe, with one company in the Firth of Thames estimating that crop losses from fish predation to cost more than $5 million NZD in lost production in one year alone (Stobart et al., 2024). As such, effective methods for deterring fish predation on Greenshell™ farms are urgently needed.

While farm-wide physical exclusion can be effective at preventing fish predation the deployment of fish exclusion nets would be challenging in the context of Greenshell™ aquaculture in New Zealand. Farms used for culturing Greenshell™ are typically located in water that is deeper (>10 m) than for mussel farms in other parts of the world where fish exclusion netting has been used, making it more difficult to enclose Greenshell™ farms entirely with netting (Jeffs et al., 1999). The arrangement of these farms consists of backbone lines up to several hundred metres long running parallel to each other in close proximity, with anchor ropes secured to the seafloor, typically covering an area of more than several hectares in size with a perimeter of around 1 km. Labour and fuel costs are major costs for mussel farm production, such that deploying nets large enough to enclose these large Greenshell™ mussel farms throughout the water column to the seafloor could create significant additional financial burdens (Jory et al., 1984; Ramšak et al., 2024). The accumulation of biofouling on these nets would also require regular cleaning and maintenance to avoid the restriction of water flow to the mussels. Such nets would also cause problems for vessel operations and face difficulties with regulatory approvals. While extensive netting placed around an entire mussel farm has been successful for reducing the impact of fish predation in Spain, this approach has not been more widely adopted in the region beyond experimentation, most likely due to the physical and regulatory challenges mentioned above. (Peteiro et al., 2010).

Currently, the seeding of Greenshell™ farms involves the deployment of seed mussels alongside a filamentous plastic dropper rope, which is then held enclosed with a protective stocking that is usually knitted from cotton, or a cotton-synthetic fibre blend. This stocking holds the rope and seed mussels together, allowing time for the seed mussels to attach to the rope before the cotton stocking degrades, leaving only the mussels attached to the rope (Skelton and Jeffs, 2020; Skelton and Jeffs, 2021). The weave and materials used to fabricate stockings varies across the industry, but they are most commonly woven with small (<10 mm) holes designed to maintain water flow to the mussels and purportedly provide some level of protection from predatory fishes. However, these stockings degrade and often become indistinguishable apart from individual strands within 7 weeks of seeding (Skelton and Jeffs, 2020), and the structural integrity of different stockings can vary considerably. Therefore, it is possible that modifications to these protective cotton stockings might be able to enhance their longevity and provide an additional means of physically excluding fish from predating upon mussels contained inside. If a stocking can resist attacks from fish or maintain its integrity longer than a few weeks after mussels are seeded on to dropper ropes, it may provide sufficient time for the mussels to become well established and more able to resist fish predation pressures on their own. Stockings have been shown to be effective at reducing losses to predation in some applications, such as reducing blue mussel losses caused by diving ducks by up to 31% (Dionne et al., 2006). However, there is no published research examining the ability of mussel stocking to provide protection against predatory fish.

The aim of this study was to test the effectiveness of two new anti-predation cotton stockings from Lock Sock® (Lock Sock® Combo 42 Needle and a proprietary Polycotton blend), at preventing fish predation on Greenshell™ farms. These two stockings were tested against an industry standard stocking in New Zealand, provided by Quality Equipment Ltd. These three stockings were tested to determine the potential for an inexpensive, but effective method to exclude fish and mitigate mussel losses caused by fish predation This research utilized dropper ropes seeded with juvenile interseed mussels (45-60 mm mean shell length, SL). This intermediate size was chosen due to previous work which observed that fish tend to target mussels within this size range in the Firth of Thames (Stobart et al., 2024).

2. Materials and Methods

2.1. Study site and source of mussels

This study was conducted from 3 April to 15 May 2024, on a coastal Greenshell™ farm in Manaia Harbour (36° 50' 56.8"S, 175° 26' 58.6"E) within the Firth of Thames of the Coromandel Peninsula, in northern New Zealand (Fig. 1). The experiment was deployed at the same time as commercial mussel farmers were undertaking the interseeding process, which involves mechanically stripping juvenile mussels from the seeded dropper ropes, before reseeding them at lower densities to maximise their subsequent growth and survival.

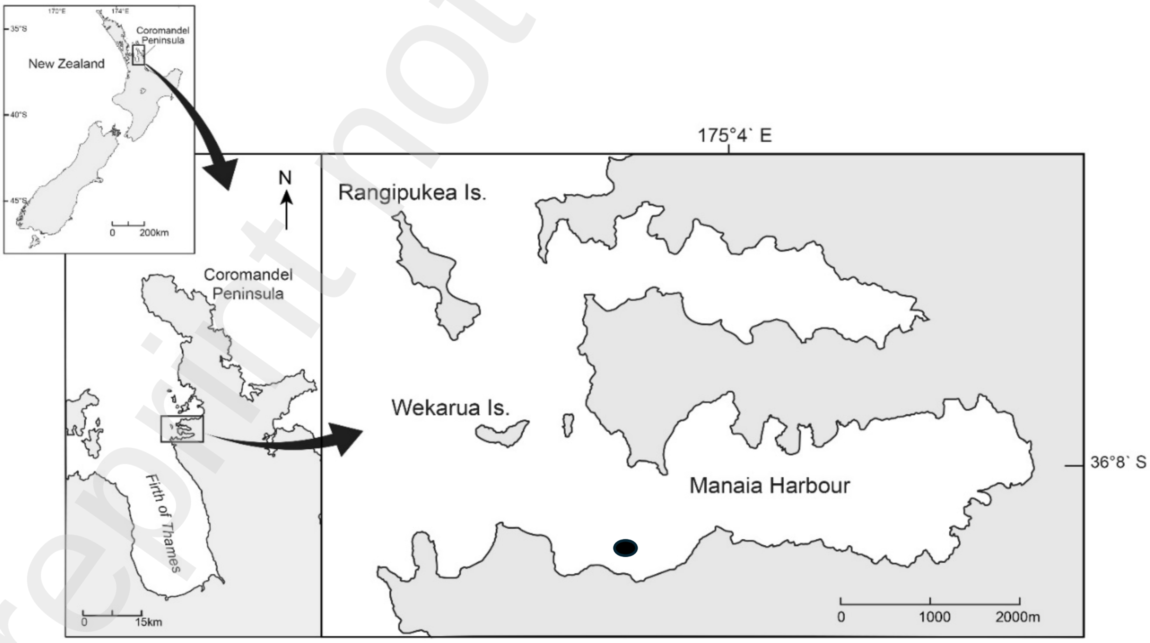

Fig. 1. Map of New Zealand and the Coromandel Peninsula, showing the location of the study site in Manaia Harbour, within the Firth of Thames.

2.2. Experimental design

2.2.1. Stocking treatments

To assess the effectiveness of stockings at mitigating fish predation on Greenshell™ farms, juvenile mussels (i.e., between 45 and 60 mm shell length) were reseeded onto three 100 m sections of mussel dropper rope, each encased in one of three types of stocking; 1) Standard Polycotton - a polycotton stocking routinely used by the Greenshell™ industry during interseeding (Quality Equipment Ltd, Polycotton 85:15 blend in 54 needle), 2) Anti-Predation (AP) stocking (Lock Sock Combo in 42 needle, Lock Sock®), comprised of two different grades of cotton designed to degrade at varying rates to maintain shape and enhance protection from predatory fishes, and 3) Hatchery Polycotton- a polycotton stocking (Lock Sock Hatchery Sock, Lock Sock®), not previously tested during the interseeding stage of Greenshell™ mussel aquaculture. Once seeded out, each 100 m section of seeded dropper rope was then tied to the backbone line of the mussel farm, with looped dropper ropes spaced 2 m apart.

2.2.2. Predator exclusion treatments

Each seeded length of dropper rope was further divided into three randomly assigned predator protection treatments: 1) Control – consisting only of the seeded dropper rope encased in one of the three types of stocking, designed to compare the anti-predation capabilities of the three stockings when exposed to full fish predation, 2) Partial cage– consisting of plastic mesh cages with sections cut out designed to partially exclude predatory fishes from the stocking encased seeded dropper rope while accounting for any potential cage effects caused by the cages in the full caged treatment, and 3) Full cage – consisting of intact plastic mesh cages designed to fully exclude fish predation from the stocking encased seeded dropper rope.

The cages used in the Full cage treatments consisted of 1.5 m long × 0.25 m diameter cylinders constructed from black plastic mesh (20 mm mesh aperture) with a 50 mm diameter hole cut out at each end, designed to enable them to be fitted around the seeded ropes. The cages were securely held in place on the ropes with cable ties at each end. The cages used in the Partial cage treatments were identical to those used in the Full cage treatments except for five 50 × 100 mm sections cut out of the plastic mesh, designed to provide partial protection to the enclosed mussels from larger fish, but account for any potential confounding effects observed when using full exclusion cages, such as increased biofouling and water flow restriction (Jory et al., 1984; Stobart et al., 2024). The patterns of sections cut out of the Partial cages were consistent among all the Partial cages used.

Replicates of the three cage treatments were placed at random positions along each of the three 100 m lengths of seeded rope encased with the three types of stocking. At least 1.5 m of seeded rope were left between each replicate, to reduce any confounding effects of neighbouring replicates. Due to logistical problems encountered on the mussel seeding barge, fewer Full and Partial cage replicates were used in the Standard Polycotton and Hatchery Polycotton treatments. In the case of the Standard Polycotton treatment, 12 cages (six Full and six Partial) were used, and in the case of the Hatchery Polycotton treatment, six cages (three Full and three Partial) were used. In the case of the AP stocking nine replicates of both Full and Partial cages and the Control were deployed. All replicates, regardless of treatment, were deployed on the mussel farm at depths between 3-8 m below the surface of the water, excluding the very top and bottom sections of the rope.

2.3. Sampling protocol

Three randomly selected replicate sections (i.e., 1.5 m lengths) of seeded rope from each of the three types of stocking were retained at the outset of the experiment (Day 0) to enable initial measurements of the seeded mussels and the dry weight of cotton seeded onto each of the experimental replicates. However, due to constraints encountered during seeding in the lengths of available AP and Hatchery Polycotton stockings, only the 1.5 m of the Standard Polycotton stocking was available to be dried and weighed for an Outset weight.

Further samples from each treatment were retrieved from the farm after 12 days (Sample 1), 31 days (Sample 2), and 45 days (Sample 3) in the water. For the AP stocking treatment, at each sampling event, three replicates were retrieved for the Control, Full, and Partial cage treatments. For the Standard Polycotton treatment, at each sampling event, three Control, two Full, and two Partial cage replicates were retrieved. For the Hatchery Polycotton stocking treatment three Control, one Full, and one Partial cage replicate were retrieved at each sampling event.

2.4. Mussel retention and growth

After each sampling event, the collected replicates were returned to the laboratory and cut into three separate (0.5 m) sections for subsampling and analysis. Any remaining stocking was carefully removed from each subsample, before being washed, dried in a drying oven for 24 h at 55 ˚C and subsequently weighed. All live mussels remaining attached to the rope were then carefully removed and counted.

From each replicate subsample, 38 randomly selected mussels attached to the ropes were photographed and their SL measured using image analysis (ImageJ Software). In 64 replicate subsamples where less than 38 mussels remained, all remaining mussels were measured.

2.5. Camera deployment

To gain an understanding of the species of fish present and record behaviour around seeded mussels, underwater cameras (GoPro Hero 9 on wide view settings) were deployed at the outset of the experiment and again at the first and second sampling events (i.e., days 0, 12, and 31). Two cameras were placed adjacent to the section of dropper rope seeded with Standard Polycotton and a further two adjacent to the section of the dropper rope seeded with AP stocking. The two cameras deployed adjacent to the dropper rope seeded with Standard Polycotton were positioned to record seeded replicates in a Control and a Partial cage treatment, while the cameras deployed adjacent to the dropper rope seeded with AP stocking were positioned to record Control replicates. The cameras were mounted in aftermarket plastic cases (Suptig), connected to an external battery (Suptig 5 volt) which were cable tied to PVC pipes glued together in a "T" shape (Underwood, 2023). These T frames were secured with cable ties on the longline backbone above the selected treatment, with the cameras facing downwards at an angle towards the dropper rope and set to record at a wide angle. The T frames were installed on Day 0 at 3-5 h after the seeded ropes were deployed. This provided an opportunity to inspect the seeded ropes for any obvious signs of predation that may have already occurred (Fig. 5). Once attached to the T frames and turned on, the cameras recorded continuously, up to 8 h after deployment. Cameras were retrieved the following day, with the process repeated for the subsequent two sampling events. The video recordings from the cameras were downloaded and reviewed by a researcher and a record made of observations of the fish species present and any fish interactions with the mussel dropper ropes, such as fish biting the stocking, eating mussels, and investigating the mussel dropper ropes.

2.6. Statistical analyses

Three-way analyses of variance (ANOVA) were used to compare each response variable (i.e., number of mussels remaining attached to sections of dropper rope, mussel size, number of dead mussels, and dry weight of remaining stocking) for the factors Stocking type, Cage type, and Sampling event. The parametric assumptions for ANOVA were checked by examining distribution of residuals using plots of residuals against means. The data for all four response variables were log transformed before analysis and rechecked for compliance with assumptions for parametric analyses. When all four datasets failed assumptions for normality and all but one (mussel size) failed for homogeneity of variance, they were examined using Welch's ANOVA, which is more accommodating of violations of assumptions of equality of variance. Post-hoc tests were examined using emmeans and Tukey's adjustments.

3. Results

3.1. Mussel losses

The mean initial density of mussels seeded onto the dropper ropes was 172.9 m^{-1} (± 4.1 SE) for the Standard Polycotton stocking treatment, 189.8 m^{-1} (± 1.9 SE) for the AP treatment, and 186.7 m^{-1} (± 5.0 SE) for the Hatchery Polycotton stocking treatment. Over the course of the 42 day experiment, there was a general trend of decreasing mussel retention across all stocking and cage treatment combinations (Fig. 2). In the Standard Polycotton treatment at the end of the experiment the mean number of mussels remaining attached to the dropper ropes was 33.0 m^{-1} (± 8.0 SE) in the Control treatment, 162.3 m^{-1} (± 6.0 SE) in the Full cage treatment, and 143.0 m^{-1} (± 8.3 SE) in the Partial cage treatment. This represented losses of 81.7%, 6.1% and 17.2% respectively. In the AP treatment, the mean number of mussels remaining attached to the dropper ropes was 25.8 m^{-1} (± 4.8 SE) in the Control treatment, 164.7 m^{-1} (± 6.0 SE) in the Full cage treatment, and 181.8 m^{-1} (± 8.4 SE) in the Partial cage treatment. This corresponded to losses of 86.5%, 13.3%, and 5.1% from the initial densities respectively. Similarly, in the Hatchery Polycotton treatment at day 42, the mean number of mussels remaining attached to the dropper ropes was 24.7 m^{-1} (± 4.3 SE) in the Control treatment, 170.7 m^{-1} (± 5.0 SE) in the Full cage treatment, and 158.7 m^{-1} (± 3.7 SE) in the Partial cage treatment, representing respective losses of 86.9%, 8.6% and 15.1%.

The mean number of mussels remaining attached to the dropper ropes differed significantly among sampling events, stocking types and cage treatments, as indicated by a significant three-way interaction (sampling event × cotton treatment × cage treatment; Welch's $F_{(12, 231)} = 2.063$, $P = 0.02$). Post-hoc comparisons revealed that at the outset (Day 0) of the experiment, there were no significant differences in the mean number of mussels seeded onto dropper ropes among the three stocking types. However, patterns of mussel retention emerged during subsequent sampling events, differing across stocking types and cage treatments.

For the Standard Polycotton treatment, fewer mussels remained attached in the Control treatment than the Partial and Full cage treatments for all sampling events ($P < 0.001$), with no differences between the Partial and Full cage treatments for any sampling event. In the AP treatment, fewer mussels remained attached to dropper ropes in the Control treatment compared to the Partial and Full cage treatments at all sampling events ($P < 0.05$), while no differences were observed between the Partial and Full cage treatments at any sampling event. For the Hatchery Polycotton treatment, there were fewer mussels remaining attached to dropper ropes in the Control treatment than in the Partial cage treatment at Sample 1 ($P < 0.001$), Sample 2 ($P = 0.003$), and Sample 3 ($P < 0.001$). Additionally, more mussels remained in the Full cage treatment compared to the Control treatment at Sample 2 ($P < 0.001$) and Sample 3 ($P < 0.001$). At Sample 1, more mussels remained in the Partial than in the Full cage treatment ($P = 0.01$), but by the end of the experiment, there was no differences between the Partial and Full cage treatments.

Within the Control treatment, stocking type had an impact on mussel retention during the initial sampling events. At Sample 1, the Hatchery Polycotton treatment retained more mussels than either the Standard Polycotton ($P < 0.001$) or the AP treatments ($P < 0.001$). These differences persisted at Sample 2, but were no longer significant at Sample 3, where the mean number of mussels remaining was consistent among the three stocking types. Similarly, at Sample 3, there were no differences in mussel retention among the three stocking types within the Partial or Full cage treatments ($P > 0.05$).

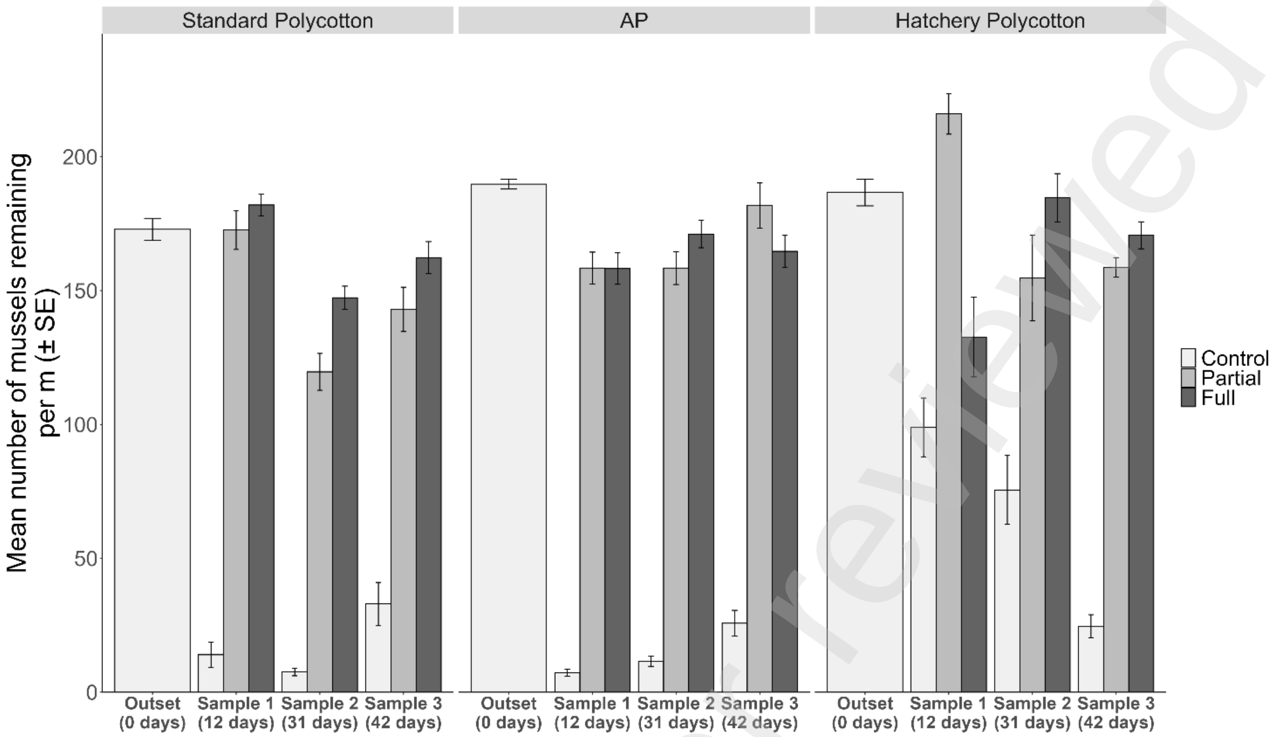

Fig. 2. Mean number of mussels (m^{-1} ± SE) remaining attached to dropper ropes in each of three stocking types and three cage treatments over the course of the 42 day experiment.

3.2. Stocking breakdown

At the outset of the experiment, the mean dry weight of stocking material used to encase the dropper ropes was and 1.99 g m^{-1} (± 0.03 SE) in the Standard Polycotton treatment but was not measured for the AP or Hatchery Polycotton treatments (Fig. 3). The mean dry weight of stocking material that remained encasing the dropper ropes differed among sampling events, stocking type, and cage treatment (i.e., sampling event × stocking treatment × cage treatment interaction, Welch's $F_{(8, 183)} = 3.0$, $P = 0.003$).

Post-hoc comparisons revealed no significant changes in the mean dry weight of the Standard Polycotton stocking material among sampling events or cage treatments ($P \geq 0.05$). In the AP treatment, at Sample 2 after 31 days, less stocking material remained on the dropper ropes in the Control treatment compared to the Full cage treatment ($P = 0.02$). After 42 days, at the end of the experiment, less material remained encasing the dropper ropes in the Control treatment than the Full cage treatment ($P < 0.001$), and also less material remained in the Partial cage treatment than the Full cage treatment ($P = 0.03$). At Sample 1, less Hatchery Polycotton stocking material remained in the Full cage treatment than the Control treatment ($P = 0.008$). At Sample 2, less Hatchery Polycotton material remained on the dropper ropes in the Control treatment than the Partial cage ($P = 0.01$) and Full cage ($P < 0.001$) treatments.

Post-hoc comparisons also indicated that, at Sample 1, in the Control treatment, more of the Hatchery Polycotton stocking remained than both the AP ($P = 0.02$) and Standard Polycotton stockings ($P < 0.001$), and more material remained in the AP treatment than the Standard Polycotton treatment ($P < 0.001$). There were no significant differences at Sample 2, but at Sample 3 in the Control treatment, more of the Standard Polycotton stocking remained than the Hatchery Polycotton ($P = 0.007$).

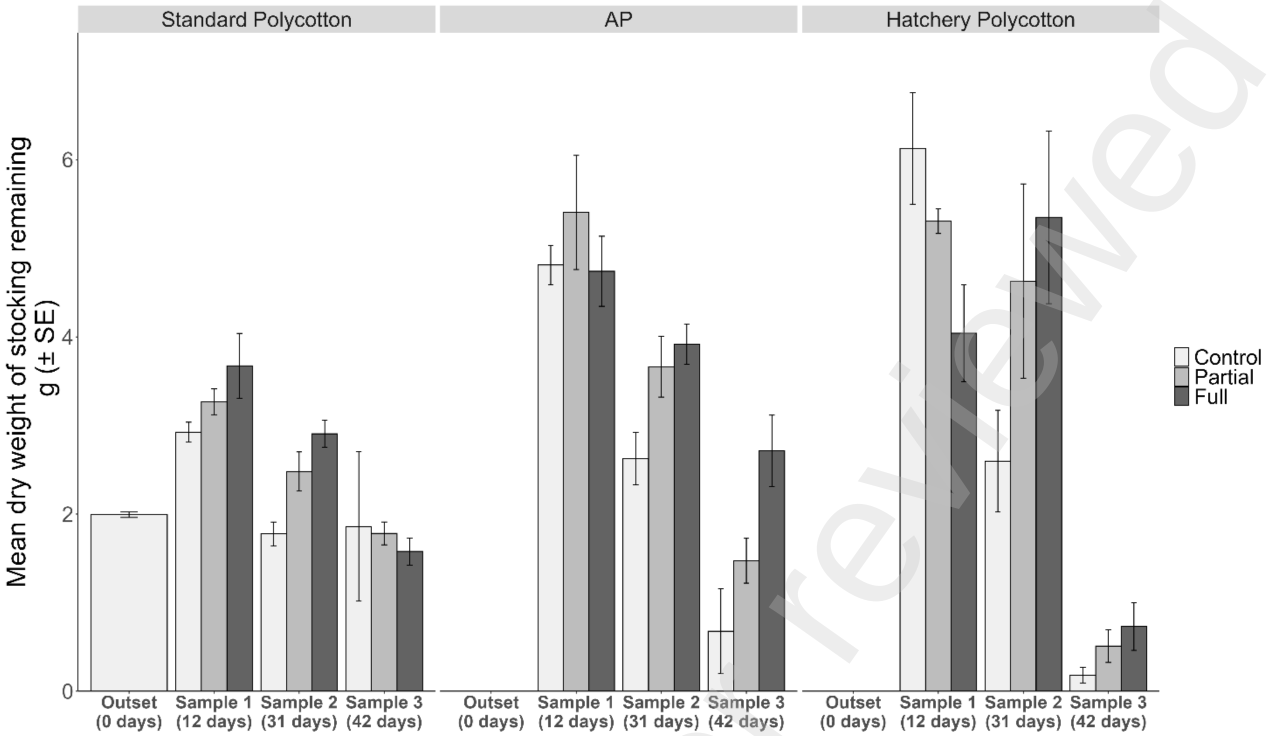

Fig. 3. Mean dry weight of stocking material (g^{-1} ± SE) remaining attached to dropper ropes in each of three stocking types and three cage treatments over the course of the 42 day experiment.

3.3. Mussel shell length

The mean size of the mussels remaining attached to the dropper ropes varied among sampling events, stocking types, and cages treatments (i.e., sampling events × stocking treatment × cage treatment interaction, Welch's $F_{(8,\,5897)} = 6.698$, $P < 0.001$). At the time of seeding, the mean size of the mussels across the three stocking treatments was 62.2 mm SL (± 0.33 SE). Over the course of the experiment, the mean size of mussels decreased from their initial size at the outset, and remained relatively stable, ranging from a low SL of 54.5 mm (± 0.27 SE) in the Partial cage treatment of the AP treatment taken at Sample 2, to a high SL of 57.3 mm SL (± 0.30 SE) in the Partial cage treatment of the AP treatment at the end of the experiment (Fig. 4). While post-hoc comparisons revealed a range of significant differences in mussel sizes among different sampling events, stocking treatments, and cage treatment combinations, the size of these differences, excluding the decrease from the outset measurements, tended to be very small (i.e., < 3 mm) (Fig. 4).

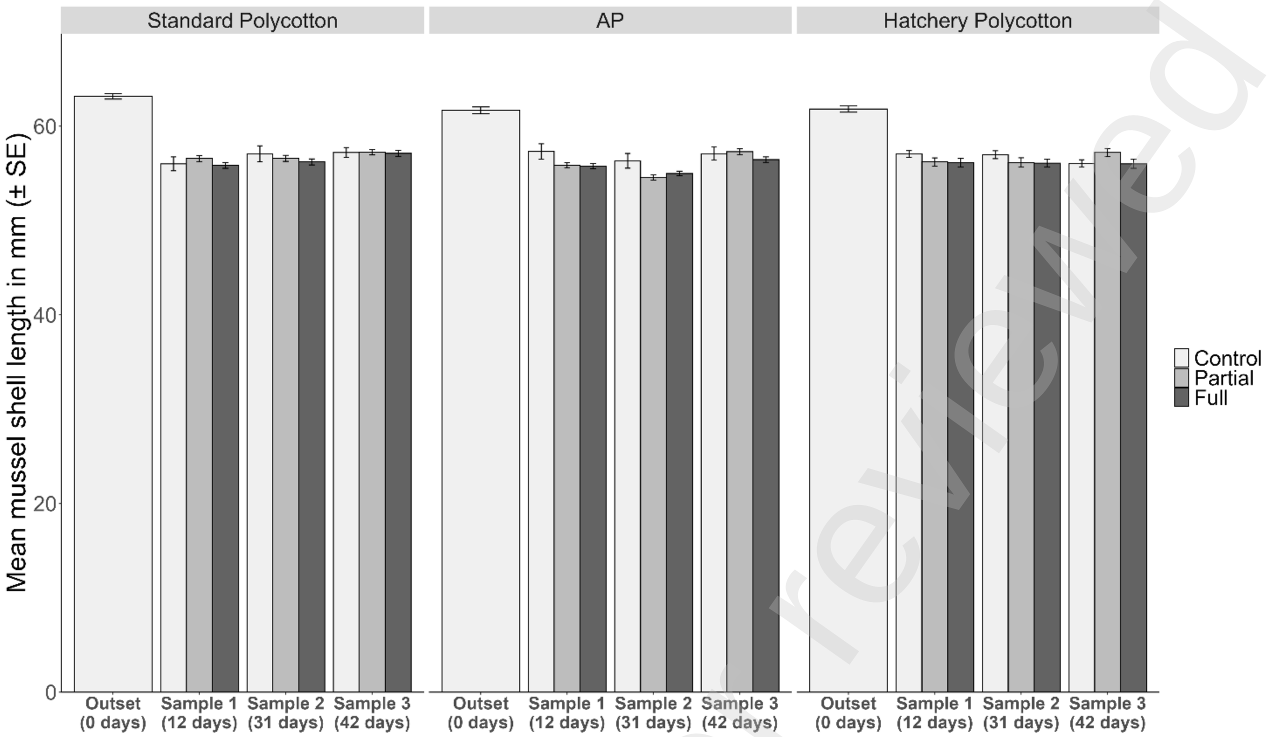

Fig. 4. Mean SL (mm ± SE) of mussels remaining attached to dropper ropes among three stocking types and three cage treatments throughout the 42 day experiment.

3.4. Observations of fish predation

In each of the three camera deployments, one to two of the external batteries failed, resulting in no more than 3-5 h of recordings per deployment.

During the 5 h of recorded video from the deployment of the experiment (i.e., Day 0), the only fish species identified interacting with the seeded dropper ropes was snapper (*C. auratus*) and no other fish species were observed around the mussel dropper ropes. Snapper activity was focused on the recently seeded dropper ropes, including biting of the seeded ropes, which continued throughout the 2-3 h duration of the recordings, including after the mussel barge had departed from the farm. Snapper interest in the newly seeded mussel ropes generally consisted of one of several behaviours, including swimming around and investigating the ropes, orienting towards and striking the ropes, and ripping holes in the stockings to access the mussels, which were then consumed. In instances where fish attacked the dropper ropes, they generally began by swimming in around a seeded rope; orienting their bodies towards a dropper rope and making sharp, repeated strikes; and most often eventually ripping a hole in the stocking surrounding the seeded dropper rope and removing a mussel or catching the mussel as it fell from the rope (Fig. 5a). Some snapper would make two or three unsuccessful attempts at tearing open the stocking, then move on to another rope out of frame. However, most snapper that made repeated strikes kept trying until they made a hole in the stocking. From these holes in the stocking, fish were then able to remove and consume individual mussels, which often occurred as the fish swam away from the rope. Observations showed mussels were taken from the rope on an individual basis (i.e. one fish would take one mussel at a time). In several instances, once a single fish had torn through the stocking, nearby fish then encircled the dropper rope and they also began feeding on the rope collectively (Fig. 5b).

No fish were observed in the total of 3 h of recordings taken from cameras deployed at Sample 1 (i.e., day 12) of the experiment, and only one snapper was observed in the total of 3 h of recordings taken at Sample 2 (i.e., day 31). This snapper was not observed to interact with the dropper ropes within camera view.

Fig. 5 a-d. Screenshots taken from camera recordings taken at/immediately following the deployment of cameras at the outset of the experiment, i.e., Day 0. From top left to right: **a.** Snapper tearing a hole in a section of dropper rope enclosed in AP stocking and removing a mussel **b.** Snapper gathering around and biting dropper rope enclosed in AP stocking and tearing at it in a circle, a behaviour observed repeatedly throughout the recordings **c-d.** Holes (red circles) in Control sections of Standard Polycotton (left) and AP (right) stockings, 3-5 h after they were seeded out with. These images were captured during the attachment of the camera frame to the mussel farm. **d.** As an example of the extent of fish predation, the number of mussels on the AP stocking treatment Control replicate in the foreground (blue circle) was reduced by 94% compared to the Outset numbers within the first 12 days in the water.

4. Discussion

4.1. Fish predation and crop losses

The findings of this study confirm that fish predation is a significant contributor to crop losses on Greenshell™ farms in northern New Zealand. Over the duration of this study (42 days), the mean number of mussels remaining attached to the unprotected Control dropper ropes (i.e., those exposed to fish predation) decreased by an average of 85% over all three types of stocking. In contrast, the mussel losses on dropper ropes that were either partially, or fully protected from fish predation averaged 12.5% and 9.3% over the 42 days, respectively. Various factors could have contributed to the observed losses of seeded mussels, such as stress from the seeding process, sudden changes in water velocity when moving from site to site, self-thinning behaviours, physical dislodgement, and biofouling (South et al., 2019; Carton et al., 2007; Hayden and Woods, 2011). However, the experimental design used in this study, which included both full and partial protection from predators, along with underwater camera observations, allows for these losses to be confidently attributed to fish predation.

These results contribute to the growing body of research highlighting the impact of fish predation on bivalve aquaculture, a problem that appears to be intensifying for bivalve farming operations worldwide. For example, fish predation has been identified as a significant contributor to the high spat losses (80 - 90%) often measured during the first year of production on unprotected Pacific oyster (*Magallana gigas*) and Mediterranean mussel (*Mytilus galloprovincialis*) farms in France (Robert and Gérard, 1999; Richard et al., 2020). Fish predation is also a major problem on mussel farms in the Adriatic Sea, where it has been shown to result in crop losses of between 54 and 90% (Šegvić-Bubić et al., 2011; Avdelas et al., 2021; Ramšak et al., 2024), and is expected to worsen in coming years due to the combination of both warming waters and escapes of bivalve-consuming gilthead seabream from nearby fish farms (Glamuzina et al., 2014; Žužul et al., 2019; Šegvić-Bubić et al., 2011). High levels of fish predation have also been identified as an impediment to the establishment of mussel aquaculture industries in India and Australia (Appukuttan, 1980; MacIntyre et al., 1977; Soundararajan et al., 1988). Collectively, these results demonstrate that bivalve producers worldwide need to develop effective methods for reducing the impacts of fish predation. This is particularly true in the case of the Greenshell™ industry in New Zealand, which is already one of the most inefficient mussel aquaculture industries in the world, losing up to 99% of mussel seed in the first few months of production, and therefore, cannot afford to sustain further crop losses due to fish predation (Skelton et al., 2022)

4.2. Physical exclusion as effective predation mitigation

The result of this current study also confirms that physical exclusion of predatory fish can be a highly effective means of reducing losses of mussels due to fish predation on mussel farms. However, when designing techniques to physically exclude fish from mussel farms, the manner in which that exclusion is achieved is extremely important. The three types of stocking used in this experiment, all of which are routinely used by the Greenshell™ industry, consistently failed to protect mussels from fish predation over the course of the experiment. Irrespective of the stocking used, when mussels were only protected by the stocking material itself (i.e., the Control treatment), and not by the addition of plastic mesh cages, losses were high, reaching up to 100% in some replicates. In contrast, when used in combination with either partial or full mesh cages, the impacts of fish predation were eliminated (i.e., ≤17.2% losses). Furthermore, given that there were only minor differences in mussel losses between partial and full cages, it does not appear that the structure of the cages themselves contributed to losses, either through mortality or reduced growth due to biofouling or restriction of water flow (Munroe et al., 2015).

These results demonstrate that while physical exclusion can work to reduce the impacts of fish predation without impacting mussel performance, careful consideration is required to determine the best approach to exclude fish. For instance, while installing anti-predator nets around the perimeter of mussel farms in France reduced losses due to fish predation, surveyed farmers still estimated up to 26% crop losses (Gervasoni and Giffon, 2016). Similarly, the experimental use of meshed netting to protect individual mussel dropper ropes from fish predation reduced crop losses by 42-62% in Spain (Peteiro et al., 2010). Therefore, in mussel farming operations, such as for the Greenshell™ industry, where the installation of perimeter nets around the farms may not be a viable option, modifications to existing farming infrastructure (e.g., stocking materials and grade) or husbandry practices might be just as, or potentially even more, effective at excluding fish. However, given that the stocking materials used in this study were ineffective at excluding fish, new, more robust alternatives will likely need to be developed.

4.3. Timing of fish predation and crop losses

Irrespective of the stocking used in this current study, most crop losses from unprotected dropper ropes took place early on within the first 12 days of seeding out. In the unprotected AP and Standard Polycotton stockings, most mussel losses (i.e., between 92 and 96% of the Outset mean) occurred within the first 12 days of seeding, with no further significant losses during the final 30 days of the experiment. A similar pattern was measured in the Hatchery Polycotton treatment, although the losses of mussels were of a smaller magnitude than for the other two stocking treatments, i.e., an average of 47% were lost within the first 12 days, 59.5% after 31 days, and 86.9% after 42 days. These results are consistent with previous research that found most losses of farmed mussels due to fish predation take place within the first 24 h to one month after seeding, regardless of mussel size or growing methods (Rilov and Schiel, 2006; Richard et al., 2020; Šegvić-Bubić et al., 2011). In this experiment, holes were observed to have been torn in the stocking in the Control treatment stockings by fish at the time of deploying the cameras (i.e., only 3-5 h after the initial seeding of mussels onto the dropper ropes), indicating immediate predation. These observations were further confirmed by the camera recordings, which showed substantial numbers of snapper investigating and biting the mussel ropes at this time. In contrast, there was an almost complete absence of fish subsequently recorded by the cameras at Sample 1 or Sample 2.

The reasons for these high initial losses of mussels, interest by fish, and differences in early performance among stockings are unclear. One possible reason for this relatively narrow window of predatory activity may be that fish are conditioned by the sights and sounds associated with barges and other farm boats to expect a sudden influx of easily obtained food (Hayden, 1995; Dempster et al., 2002; Callier et al., 2018). The interseeding process on Greenshell™ farms is characterized by bright spotlights, engine and propeller noise, and individual mussels and debris continuously falling of the boat as dropper ropes are handled and stripped. Damaged or stressed bivalves are known to emit chemical cues that possibly act as attractants for various predators (Hay, 2009; Dominguez et al., 2021). Combined, these stimuli may act as an auditory, chemical, and visual cue for fish to aggregate and follow the barges for a temporary supply of easy to access mussels. Once the newly seeded dropper ropes were stripped, or the fish had eaten to satiation, they may have moved on.

Only the Hatchery Polycotton stocking affected mussel retention for the first month (with more mussels remaining than on the AP or Standard Polycotton stockings until Sample 3), but mussel farms usually leave out newly seeded mussels for far longer lengths of time between stripping and reseeding. These results may be an indication of continued predation by fish long after the initial bout of heightened predatory activity observed immediately after the seeding of mussels. Nearly 30% of the losses of mussels from the unprotected Hatchery Polycotton treatment occurred in the final 11 days of the experiment. It is possible that fish were still actively predating on mussels from these dropper ropes and the limited camera placement simply missed the activity. As a result of the Hatchery Polycotton stocking's partial effectiveness, there were still mussels to attract predators well after the other two stocking treatments were depleted. However, on a production time scale used by farmers, typically measured in months between reseeding events, a somewhat more robust stocking that can retain mussels for a longer period and resist initial fish attack shortly after seeding mussels has the potential to significantly improve mussel retention.

Another possible reason that fish predation might disproportionately affect newly seeded mussels in the days immediately after seeding is that the mussels may not have yet oriented themselves and attached securely with their byssus threads to the growing ropes making them easier for fish to remove (George et al., 2019). Mytilid species such as Greenshell™ mussels secrete strong byssus threads to attach to structures. It is possible that the sudden water changes, atmospheric exposure, and physical handling that can occur during the transport and seeding process of mussel aquaculture disrupts byssus thread production long enough to easily allow predatory fish to remove them from the mussel dropper ropes (George et al., 2019; Knowlen et al., 2012; Carrington et al., 2015). While the byssal production process can produce adhesive within minutes of surface contact and produce strong attachments within 14 - 18 h (Knowlen et al., 2012), disruption from the stressors of aquaculture can last several days (George et al., 2019). After a period of recovery, the mussels can begin making more byssal threads and attachments that are strong enough to deter predatory fish from making the effort to remove them from the ropes. Byssus strength can increase over time and is strengthened in response to both predators and injured conspecifics (Reimer and Tedengren, 1997; Christensen et al., 2012). If a deterrent can successfully protect unattached mussels for a few days after seeding, the strength of the byssus thread attachment and density of attached mussels may be enough to significantly reduce predation losses from the dropper ropes without further input (Cheung et al., 2009). Therefore, any potential method of predatory fish deterrence may only need to be effective during the first month following seeding out.

4.4. Stocking breakdown

The stockings used during seeding of Greenshell™ farms are designed to encase newly seeded mussels on a growing rope for a long enough period to allow the mussels to settle and attach to the dropper rope (Skelton and Jeffs, 2020). While the three types of stockings tested in this experiment did not offer protection against fish for the 42 day period, they did allow any mussels remaining on the ropes sufficient time to secure byssus threads on the ropes before the stocking degraded. The three stockings also degraded at different rates. The Anti-Predation and Hatchery Polycotton stockings retained some integrity until Sample 2 (31 days), while the Standard Polycotton was already severely torn and degraded at Sample 1 (12 days) (Fig. 6), with clear indications of tears and breakdown mere hours into deployment (Fig. 5c). The Hatchery Polycotton treatment from the unprotected dropper ropes retained more mussels than the other two stockings up to Sample 2 (31 days), but retention was the same as the other two types of stocking by Sample 3 (42 days).

Fig. 6. A section of the Control Standard Polycotton stocking after 12 days (Sample 1), showing the extent of the tearing in the stocking from fish predation activity on the encased mussels.

A possible explanation for the initially better performance of the Hatchery Polycotton stocking in preventing the loss of mussels is that it does provide some limited ongoing protection against fish predation for up to a month, possibly because it is more difficult to tear. To be commercially practical, the effectiveness of a stocking in preventing fish predation depends on how long the stocking remains intact. Therefore, the initially better performance of this stocking suggests that a more robust and enduring stocking has the potential to be an effective mitigation measure for fish predation.

4.5. Size

Size selection of different sized Greenshell™ mussels by predatory fish have been observed in both natural intertidal (Rilov and Schiel, 2006) and aquaculture settings (Hayden, 1995). This experiment found some evidence of snapper preference for consuming mussels from the largest sizes in the cohort of juvenile mussels. Between the outset of the experiment and Sample 1, the overall mean SL of the mussels in the unprotected Control dropper rope replicates decreased by 5-6 mm, indicating that many mussels >60 mm were the ones selected for predation in the first 12 days of the experiment. However, this size decrease was also present in the partial and full cage treatments irrespective of stocking treatment, despite the absence of significant predation from the cages. Rather than size selective predators, perhaps this size decrease can be explained by larger mussels self-thinning and falling off of or moving away from the experimental replicates. The difference in size preference to the current study could perhaps be explained due to observed predators' lack of opportunity to consume any other size of mussels, as both the above studies only measured and used smaller and more narrowly sized cohorts (5-20 mm). Another possibility for the larger size selection seen in this experiment is that once on a seeded dropper ropes with a wide range (40-65 mm) of juvenile mussel sizes, the largest ones stand out visually and spatially to potential predators, and the snapper simply consume whichever mussel protrudes furthest from the rope. Taken together, the results from the current experiment and the two studies discussed above may also suggest a size refuge for the middle ranges (20-50 mm) of juvenile mussels.

4.6. Species responsible

This study confirms long held suspicions and anecdotal evidence that snapper are the primary species responsible for predation losses of Greenshell™ mussels. Snapper were the only fish species identified in the underwater video recordings taken during this study. Snapper have long been identified by mussel farmers in New Zealand as the primary cause of their crop losses to fish predation, but until recently there has been very little data to confirm this. Snapper were found to make up 86.6% of the total fish recorded around a Greenshell™ farm at 0-5 m depth, and an even higher percentage of fish recorded at lower depths (Stobart et al., 2024). Snapper were also recorded biting the mussel ropes more often than any other fish species. Parore (*Girella tricuspidate*) were also observed biting seeded mussel dropper ropes in this previous study, however, it was concluded this species was causing spat losses incidentally by eating the macroalgae that had been seeded out with the spat attached. In contrast, snapper were found to be the primary predator of mussels more than 20 mm in length (Stobart et al., 2024). The total absence of any observations of parore in the current study may be due to the lack of macroalgae seeded onto the mussel dropper ropes used here. Snapper are likely the predominant predators of Greenshell™ mussels of all size classes within mussel farms (Underwood et al., 2023).

These findings on snapper predation are consistent with observations of mussel predation from aquaculture by fishes elsewhere in the world, where other members of Sparidae are considered the primary species responsible (Brehmer et al., 2003). For example, black bream (*Spondyliosoma canthaturs*) in northern Spain (Peteiro et al., 2010), black seabream (*Acanthopagrus schlegelii*) and red snapper (*Pagrus major*) in Japan (Saito et al., 2008; Kawai et al., 2021), western Atlantic sea bream (*Archosargus rhomboidalis*) in Brazil (Suplicy, 2017), and gilthead seabream (*Sparus aurata*) in the Mediterranean Sea (Šegvić-Bubić et al., 2011) have all been identified as the predominant predatory fish found on mussel farms. Sparids are generalist feeders that are attracted to easily obtainable food as well as the extra three-dimensional structures offered by various aquaculture operations (Morrisey et al., 2006; Underwood and Jeffs, 2023). There are also indications that snapper will move into farming areas and become permanent residents (Underwood et al., 2024).

4.7. Conclusions

The results of this study confirm the varying efficacy of different forms of physical protection for reducing the losses of mussels from aquaculture due to fish predation. Three types of stockings used for seeding juvenile Greenshell™ mussels in New Zealand were found to be ineffective at preventing fish predation of the mussels on a production time scale. Snapper, the only fish predator observed, were readily able to tear open two of the stockings immediately upon seeding to access the mussels, and the third in just over one month. In contrast, plastic mesh cages places around the seeded mussel dropper ropes were highly effective at preventing fish predation of the juvenile mussels. Therefore, any effective physical deterrent to fish predation of juvenile mussels must be sufficiently strong to resist attack by snapper for the entire growout process.

5. Acknowledgements

Funding and support for this project was provided by the Aotearoa New Zealand Ministry for Primary Industries Sustainable Food Fund (SFF #22074). Special thanks to Gulf Mussel Farms LTD. and Allan Bartrom for the use of the Manaia harbour farm site, barge, and personal boat for deployment and sampling. Thanks to Rebecca Stobart, Andy Jordan, Emanuel Ram, Brad Skelton, and Andrew Jeffs for various field and laboratory assistance.

6. References

Anderson, E. J., Dettmers, J. M., Diana, J., McCormack, K., Morris, J. A., Scarfe, D. F., ... and Stein, R. A. (2015). Great lakes netpen commercial aquaculture: a short summary of science. *Ann Arbor, MI: Michigan Department of Environmental Quality, Michigan Department of Agriculture and Rural Development, Michigan Department of Environmental Resources*.

Appukuttan, K. K. (1980). Predation on mussels in culture by Silver Bream, *Rhabdosargus sarba*. *CMFRI Bulletin*, *29*, 44-45.

Avdelas, L., Avdic-Mravlje, E., Borges Marques, A. C., Cano, S., Capelle, J. J., Carvalho, N., ... and Asche, F. (2021). The decline of mussel aquaculture in the European Union: causes, economic impacts and opportunities. *Reviews in Aquaculture*, *13*(1), 91-118. https://doi.org/10.1111/raq.12465

Belle, S. M., and Nash, C. E. (2008). Better Management Practices for Net-Pen Aquaculture. In *Environmental best management practices for aquaculture /* (pp. 261–330). Wiley-Blackwell; https://doi.org/10.1002/9780813818672.ch8

Branco, P., Amaral, S. D., Ferreira, M. T., and Santos, J. M. (2017). Do small barriers affect the movement of freshwater fish by increasing residency?. *The Science of the total environment*, *581*, 486-494. https://doi.org/10.1016/j.scitotenv.2016.12.156

Brehmer, P. (2003). New applications of hydroacoustic methods for monitoring shallow water aquatic ecosystems: the case of mussel culture grounds. *Aquatic Living Resources.*, *16*(3), 333–338. https://doi.org/10.1016/S0990-7440(03)00042-1

Bullen, C., and Carlson, T. (2003). Non-physical fish barrier systems: their development and potential applications to marine ranching. *Reviews in Fish Biology and Fisheries.*, *13*(2), 201–212. https://doi.org/10.1023/B:RFBF.0000019481.10670.94

Callier, M. D., Byron, C. J., Bengtson, D. A., Cranford, P. J., Cross, S. F., Focken, U., Jansen, H. M., Kamermans, P., Kiessling, A., Landry, T., O'Beirn, F., Petersson, E., Rheault, R. B., Strand, Ø., Sundell, K., Svåsand, T., Wikfors, G. H., and McKindsey, C. W. (2018). Attraction and repulsion of mobile wild organisms to finfish and shellfish aquaculture: a review. *Reviews in Aquaculture*, *10*(4), 924–949. https://doi.org/10.1111/raq.12208

Carton, A., Jeffs, A., Foote, G., Palmer, H., and Bilton, J. (2007). Evaluation of methods for assessing the retention of seed mussels (*Perna canaliculus*) prior to seeding for grow-out. *Aquaculture.*, *262*(2–4), 521–527. https://doi.org/10.1016/j.aquaculture.2006.11.026

Carrington, E., Waite, J. H., Sarà, G., and Sebens, K. P. (2015). Mussels as a Model System for Integrative Ecomechanics. *Annual Review of Marine Science*, *7*(1), 443–469. https://doi.org/10.1146/annurev-marine-010213-135049

Cheung, S., Yang, F., Chiu, J., Liu, C., and Shin, P. (2009). Anti-predator behaviour in the green-lipped mussel (*Perna viridis*): byssus thread production depends on the mussel's position in clump. *Marine Ecology Progress Series.*, *378*, 145–151. https://doi.org/10.3354/meps07874

Christensen, H. T., Dolmer, P., Petersen, J. K., and Tørring, D. (2012). Comparative study of predatory responses in blue mussels (*Mytilus edulis* L.) produced in suspended long line cultures or collected from natural bottom mussel beds. *Helgoland Marine Research.*, *66*(1), 1–9. https://doi.org/10.1007/s10152-010-0241-0

Cooke, S. J., Bergman, J. N., Twardek, W. M., Piczak, M. L., Casselberry, G. A., Lutek, K., Dahlmo, L. S., Birnie-Gauvin, K., Griffin, L. P., Brownscombe, J. W., Raby, G. D., Standen, E. M., Horodysky, A. Z., Johnsen, S., Danylchuk, A. J., Furey, N. B., Gallagher, A. J., Lédée, E. J., Midwood, J. D., and Gutowsky, L. F. (2022). The movement ecology of fishes. *Journal of Fish Biology.*, *101*(4), 756–779. https://doi.org/10.1111/jfb.15153.

Cupp, A. R., Brey, M. K., Calfee, R. D., Chapman, D. C., Erickson, R., Fischer, J., Fritts, A. K., George, A. E., Jackson, P. R., Knights, B. C., Saari, G. N., and Kočovský, P. M. (2021). Emerging control strategies for integrated pest management of invasive carps. *Journal of Vertebrate Biology.*, *70*(4). https://doi.org/10.25225/jvb.21057

Dégremont, L., Ernande, B., Bédier, E., and Boudry, P. (2007). Summer mortality of hatchery-produced Pacific oyster spat (*Crassostrea gigas*). I. Estimation of genetic parameters for survival and growth. *Aquaculture.*, *262*(1), 41–53. https://doi.org/10.1016/j.aquaculture.2006.10.025

Dempster, T., Sanchez-Jerez, P., Bayle-Sempere, J., Giménez-Casalduero, F., and Valle, C. (2002). Attraction of wild fish to sea-cage fish farms in the south-western Mediterranean Sea: spatial and short-term temporal variability. *Marine Ecology Progress Series.*, *242*, 237–252. https://doi.org/10.3354/meps242237

Dionne, M., Lauzon-Guay, J.-S., Hamilton, D. J., and Barbeau, M. A. (2006). Protective socking material for cultivated mussels: a potential non-disruptive deterrent to reduce losses to diving ducks. *Aquaculture International: Journal of the European Aquaculture Society.*, *14*(6), 595–613. https://doi.org/10.1007/s10499-006-9058-x

Domínguez, R., Vázquez, E., Smallegange, I. M., Woodin, S. A., Wethey, D. S., Peteiro, L. G., and Olabarria, C. (2021). Predation risk increases in estuarine bivalves stressed by low salinity. *Marine Biology*, *168*(8). https://doi.org/10.1007/s00227-021-03942-8

FAO, IFAD, UNICEF, WFP and WHO. 2024. The State of Food Security and Nutrition in the World 2024. Repurposing food and agricultural policies to make healthy diets more affordable. Rome, FAO. https://doi.org/10.4060/cc0639en

George, G. J., Brown, K. M., Peterson, G. W., and Thompson, B. A. (2008). Removal of Black Drum on Louisiana Reefs to Increase Survival of Eastern Oysters *Crassostrea virginica*. *North American Journal of Fisheries Management.*, *28*(6), 1802–1811. https://doi.org/10.1577/M08-036.1

George, M. N., Andino, J., Huie, J., and Carrington, E. (2019). Microscale pH and Dissolved Oxygen Fluctuations within Mussel Aggregations and Their Implications for Mussel Attachment and Raft Aquaculture. *Journal of Shellfish Research.*, *38*(3). https://doi.org/10.2983/035.038.0329

Gervasoni, E. and Giffon, C., 2016. La conchyliculture en Occitanie. Résultats d'une enquête menée auprès de 135 entreprises conchylicoles. *CEPRALMAR*.

Glamuzina, B., Pešić, A., Joksimović, A., Glamuzina, L., Matić-Skoko, S., Conides, A., Klaoudatos, D., and Zacharaki, P. (2014). Observations on the increase of wild gilthead seabream, *Sparus aurata* abundance, in the eastern Adriatic Sea: problems and opportunities. *International Aquatic Research*, *6*(3), 127–134. https://doi.org/10.1007/s40071-014-0073-7

Green-Gavrielidis, L., MacKechnie, F., Thornber, C., and Gomez-Chiarri, M. (2018). Bloom-forming macroalgae (Ulva spp.) inhibit the growth of co-occurring macroalgae and decrease eastern oyster larval survival. *Marine Ecology Progress Series.*, *595*, 27–37. https://doi.org/10.3354/meps12556

Hay, M. E. (2009). Marine Chemical Ecology: Chemical Signals and Cues Structure Marine Populations, Communities, and Ecosystems. *Annual Review of Marine Science*, *1*(1), 193–212. https://doi.org/10.1146/annurev.marine.010908.163708

Hayden, B. J. (1995). Factors affecting recruitment of farmed greenshell mussels*, Perna canaliculus (Gmelin) 1791*, in Marlborough Sounds (Doctoral dissertation, University of Otago).

Hayden, B. J., and Woods, C. M. C. (2011). Effect of water velocity on growth and retention of cultured Greenshell™ mussel spat, *Perna canaliculus (Gmelin), 1791*. *Aquaculture International: Journal of the European Aquaculture Society.*, *19*(5), 957–971. https://doi.org/10.1007/s10499-010-9413-9

Jeffs, A. G., Holland, R. C., Hooker, S. H., and Hayden, B. J. (1999). Overview and bibliography of research on the greenshell mussel, *Perna canaliculus*, from New Zealand waters. *Journal of Shellfish Research*, *18*(2), 347–360.

Jory, D. E., Carriker, M. R., and Iversen, E. S. (1984). Preventing predation in molluscan mariculture: an overview. *Journal of the World Mariculture Society.*, *15*(1–4), 421–432. https://doi.org/10.1111/j.1749-7345.1984.tb00176.x

Kawai, K., Fujita, H., Sanchez, G., and Umino, T. (2021). Oyster farms are the main spawning grounds of the black sea bream *Acanthopagrus schlegelii* in Hiroshima Bay, Japan. *PeerJ.*, *9*. https://doi.org/10.7717/peerj.11475

Knowlen, M., Blattenbauer, A., and Newcomb, L. (2012). Temperature effects on byssal thread production in the mussel, *Mytilus trossulus*.

MacIntyre, R. J., Murray, P. J., Pregenzer, C., and Stoddart, H. E. (1977). Experimental Mussel Culture in Australia. *Proceedings of the ... Annual Meeting /*, *8*(1–4), 411–425. https://doi.org/10.1111/j.1749-7345.1977.tb00133.x

Maes, J., Turnpenny, A. W. H., Lambert, D. R., Nedwell, J. R., Parmentier, A., and Ollevier, F. (2004). Field evaluation of a sound system to reduce estuarine fish intake rates at a power plant cooling water inlet. *Journal of Fish Biology.*, *64*(4), 938–946. https://doi.org/10.1111/j.1095-8649.2004.00360.x

Meira, A., Byers, J. E., and Sousa, R. (2024). A global synthesis of predation on bivalves. *Biological Reviews of the Cambridge Philosophical Society.*, *99*(3), 1015–1057. https://doi.org/10.1111/brv.13057

Michaud, D., and Taft, E. (2000). Recent evaluations of physical and behavioural barriers for reducing fish entrainment at hydroelectric plants in the upper Midwest. *Environmental Science and Policy.*, *3*, 499–512. https://doi.org/10.1016/S1462-9011(00)00077-0

Morrisey, D., Cole, R., Davey, N., Handley, S., Bradley, A., Brown, S., and Madarasz, A. (2006). Abundance and diversity of fish on mussel farms in New Zealand. *Aquaculture.*, *252*(2–4), 277–288. https://doi.org/10.1016/j.aquaculture.2005.06.047

Munroe, D., Kraeuter, J., Beal, B., Chew, K., Luckenbach, M., and Peterson, C. P. (2015). Clam predator protection is effective and necessary for food production. *Marine Pollution Bulletin.*, *100*(1), 47–52. https://doi.org/10.1016/j.marpolbul.2015.09.042

Noatch, M. R., and Suski, C. D. (2012). Non-physical barriers to deter fish movements. *Environmental Reviews = Dossiers Environnement.*, *20*(1), 71–82. https://doi.org/10.1139/a2012-001

Peteiro, L. G., Filgueira, R., Labarta, U., and Fernández-Reiriz, M. J. (2010). The role of fish predation on recruitment of *Mytilus galloprovincialis* on different artificial mussel collectors. *Aquacultural Engineering.*, *42*(1), 25–30. https://doi.org/10.1016/j.aquaeng.2009.09.003

Ramšak, A., Bizjak, T., Robič, U., and Viršek, M. K. (2024). The need for innovations to secure the future of artisanal mussel farming in the coastal sea of the Gulf of Trieste (Slovenia). *Aquaculture Reports.*, *36*. https://doi.org/10.1016/j.aqrep.2024.102166

Reimer, O., and Tedengren, M. (1997). Predator-induced changes in byssal attachment, aggregation and migration in the blue mussel, *Mytilus edulis*. *Marine and Freshwater Behaviour and Physiology.*, *30*(4), 251–266. https://doi.org/10.1080/10236249709379029

Richard, M., Forget, F., Mignucci, A., Mortreux, S., Le Gall, P., Callier, M., Weise, A., McKindsey, C., and Bourjea, J. (2020). Farmed bivalve loss due to seabream predation in the French Mediterranean Prevost Lagoon. *Aquaculture Environment Interactions International and Multidisciplinary Journal.*, *12*, 529–540. https://doi.org/10.3354/aei00383

Rilov, G., and Schiel, D. (2006). Trophic linkages across seascapes: subtidal predators limit effective mussel recruitment in rocky intertidal communities. *Marine Ecology Progress Series.*, *327*, 83–93. https://doi.org/10.3354/meps327083

Robert, R. and Gérard, A. (1999). Bivalve hatchery technology: The current situation for the Pacific oyster and the scallop in France. *Aquatic Living Resources.*, *12*(2), 121–130. https://doi.org/10.1016/S0990-7440(99)80021-7

Saito, H., Nakanishi, Y., Shigeta, T., Umino, T., Kawai, K., and Imabayashi, H. (2008). Effect of predation of fishes on oyster spats in Hiroshima Bay. *Nippon Suisan Gakkaishi [[ニホンスイサンガッカイシ]]*, *74*(5), 809–815. https://doi.org/10.2331/suisan.74.809

Šegvić-Bubić, T., Grubišić, L., Karaman, N., Tičina, V., Jelavić, K. M., and Katavić, I. (2011). Damages on mussel farms potentially caused by fish predation—Self service on the ropes? *Aquaculture.*, *319*(3–4), 497–504. https://doi.org/10.1016/j.aquaculture.2011.07.031

Skelton, B. M., and Jeffs, A. G. (2020). The importance of physical characteristics of settlement substrate to the retention and fine-scale movements of *Perna canaliculus* spat in suspended longline aquaculture. *Aquaculture.*, *521*, 735054. https://doi.org/10.1016/j.aquaculture.2020.735054

Skelton, B. M., and Jeffs, A. G. (2021). An assessment of the use of macroalgae to improve the retention of Greenshell™ mussel (*Perna canaliculus*) spat in longline culture. *Aquaculture International: Journal of the European Aquaculture Society.*, *29*(4), 1683–1695. https://doi.org/10.1007/s10499-021-00710-9

Skelton, B. M., South, P. M., and Jeffs, A. G. (2022). Inefficiency of conversion of seed into market-ready mussels in New Zealand's Greenshell™ mussel (*Perna canaliculus*) industry. *Aquaculture.*, *560*, 738584. https://doi.org/10.1016/j.aquaculture.2022.738584

Soundararajan, R., Dorairaj, K., and Jagadis, I. (1988). Experimental culture of green mussel, *Perna viridis* (Linnaeus) in the Andamans. *Journal of Andaman Science Association*, *4*(1), 61-66.

South, P. M., Floerl, O., and Jeffs, A. G. (2019). The role of biofouling development in the loss of seed mussels in aquaculture. *Biofouling.*, *35*(2), 259–272. https://doi.org/10.1080/08927014.2019.1596261

South, P. M., Floerl, O., and Jeffs, A. G. (2020). Magnitude and timing of seed losses in mussel (*Perna canaliculus*) aquaculture. *Aquaculture.*, *515*, 734528. https://doi.org/10.1016/j.aquaculture.2019.734528

South, P. M., Floerl, O., and Jeffs, A. G. (2021). Immersion can trigger detachment of juvenile mussels. *Aquaculture.*, *538*, 736548. https://doi.org/10.1016/j.aquaculture.2021.736548

Stobart, R. L., Jeffs, A., Hillman, J. R., and Skelton, B. M., 2024. Identifying the Fish Species Responsible for Crop Losses in New Zealand's Greenshell™ Mussel (*Perna Canaliculus*) Farms. *Available at SSRN 4754199*. https://doi.org/10.2139/ssrn.4754199

Suplicy, F. M. (2017). Cultivo de mexilhões: sistema contínuo e mecanizado. *Florianópolis: Epagri*, *124*.

Thomas, S. N. (2009). Netting specifications and maintenance of cages for finfish culture. *NATIONAL TRAINING ON CAGE CULTURE OF SEABASS.*

Underwood, L. H. (2023). Habitat value of green-lipped mussel (*Perna canaliculus*) farms for fish in northern Aotearoa New Zealand (Doctoral dissertation, University of Auckland).

Underwood, L., and Jeffs, A. (2023). Settlement and recruitment of fish in mussel farms. *Aquaculture Environment Interactions International and Multidisciplinary Journal.*, *15*, 85–100. https://doi.org/10.3354/aei00454

Underwood, L. H., van der Reis, A., and Jeffs, A. G. (2023). Diet of snapper (*Chrysophrys auratus*) in green-lipped mussel farms and adjacent soft-sediment habitats. *Aquaculture, Fish and Fisheries*, *3*(3), 268–286. https://doi.org/10.1002/aff2.113

Underwood, L. H., Mugica, M., and Jeffs, A. G. (2024). Feasting in mussel farms fattens up snapper (*Chrysophrys auratus*) compared to snapper in adjacent natural habitats. *Aquaculture, Fish and Fisheries*, *4*(2). https://doi.org/10.1002/aff2.155

Žužul, I., Šegvić-Bubić, T., Talijančić, I., Džoić, T., Lepen Pleić, I., Beg Paklar, G., Ivatek-Šahdan, S., Katavić, I., and Grubišić, L. (2019). Spatial connectivity pattern of expanding gilthead seabream populations and its interactions with aquaculture sites: a combined population genetic and physical modelling approach. *Scientific Reports*, *9*(1), 14718–14. https://doi.org/10.1038/s41598-019-51256-z