ENHANCEMENT OF NEW ZEALAND BLACKFOOT ABALONE (*HALIOTIS IRIS*) POPULATIONS AFFECTED BY LARGE-SCALE EARTHQUAKE DISTURBANCE AND MASS-MORTALITY

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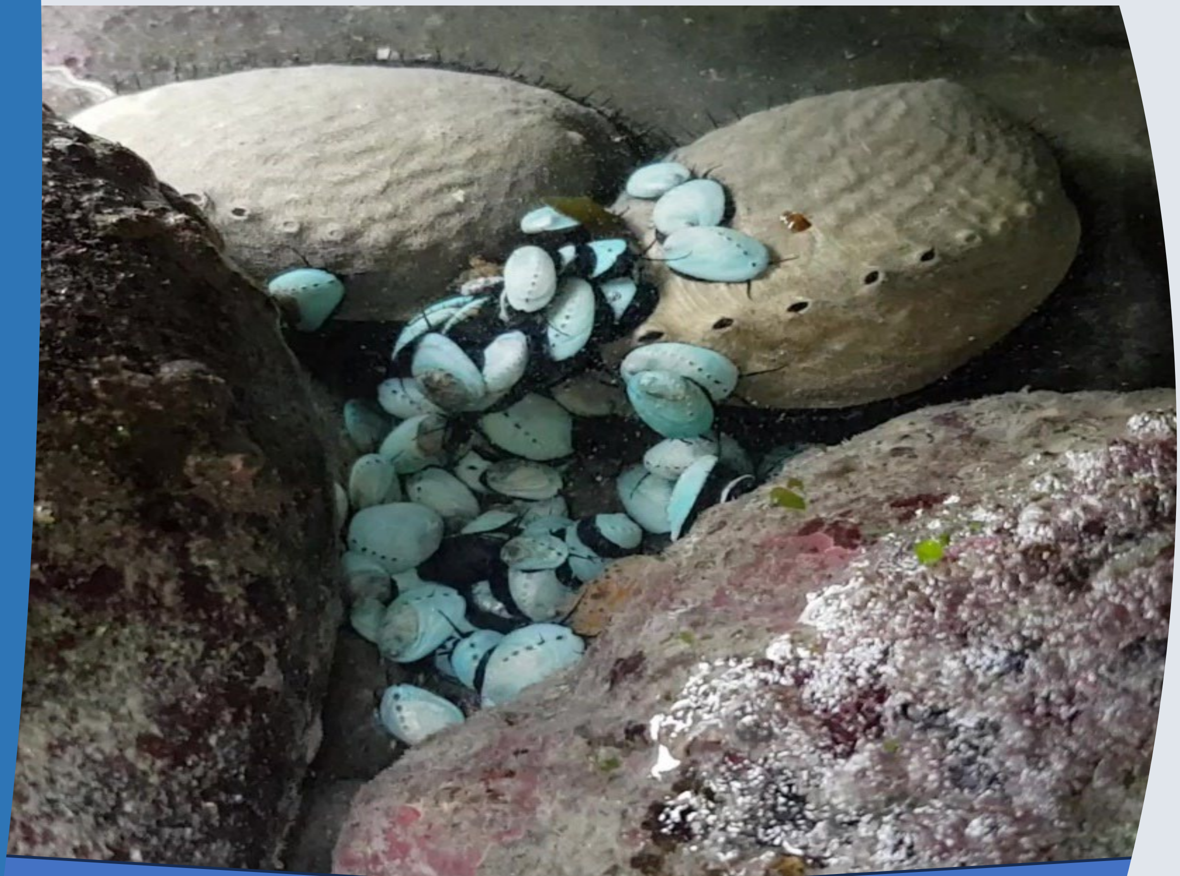

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Summary

Abalone stocks have collapsed worldwide due to overfishing, disease and environmental stressors. New Zealand is fortunate in having one of the last remaining viable wild abalone fisheries. This fishery, focused mostly on the endemic blackfoot abalone *Haliotis iris* (i.e., pāua), supports valuable customary, commercial, and recreational harvests. However, the sustainability of New Zealand's wild pāua fishery is increasingly threatened by recreational overharvesting, adverse environmental conditions and stochastic events. This has prompted a large investment by the commercial seafood sector to enhance pāua stocks. With the exception of a small amount of scientific literature and anecdotal evidence, there are few quantitative data on the efficacy of current stock enhancement methods, how to optimise them, or if modifications might be more suitable and effective.

This research program used multi-year field surveys and experimental work to assess commercial pāua stock enhancement efforts and to test novel methods. Primarily, the focus was on assessing the 2018 commercial outplanting of 167,000 hatchery-raised "seed" pāua at sites along the Kaikōura coastline. These seed pāua were outplanted in response to the cataclysmic 2016 Kaikōura earthquake, which caused high mortality of pāua, loss of critical habitats, and a 5-year closure of the very productive fishery. Our annual field surveys of 7 enhancement sites over 4 years provide one of the only data sets in New Zealand to follow the long-term abundance and growth of outplanted hatchery pāua. Outplanted pāua were visually identified up to 3 years after their release into the wild, after which they emerged from cryptic habitats and became difficult to distinguish from wild stock, or migrated to deeper habitats. The recapture rate of seed pāua was affected by movement away from seeding sites, potential mortality, and to the unexpected, prolific natural recruitment that occurred during the study. However, seed pāua made up as much as 40% of the population at some sites, and averaged 12% of populations across all sites after 3 years. This suggests that the outplanted seed pāua contributed considerably to overall pāua abundance and rebuilding of pāua stocks.

Growth rates of outplanted seed pāua were typically high (33-40 mm yr^{-1}) for the first two years, before decreasing to c. 25 mm yr^{-1} in subsequent years. These growth rates are greater than or equal to those of naturally recruited pāua in good habitat. After 3 years many of the outplanted seed pāua that had been recaptured had potentially reached sexual maturity ($\geq$82 mm shell length). The sites with the greatest density of wild pāua, however, had the slowest growth rates for seed pāua. Furthermore, of the 7 seeded sites, 2 were greatly affected by gravel inundation after storms, which buried juvenile habitats and caused high mortality of seed and wild pāua. This reinforces the importance of appropriate site selection for outplanting and choosing multiple sites to spread the risk associated with stochastic events. The insights from this research, which could be achieved only through detailed multi-year field studies, help clarify the benefits, limitations, utility and likely financial returns of stock enhancement efforts to the fishery using hatchery-raised juveniles.

The second component of this program was to experimentally test larval outplanting, the release of competent swimming pāua larvae into natural habitats, for use in stock

enhancement. This required learning hatchery techniques, inducing mature pāua to spawn synchronously, and rearing and settling resultant larvae. We spent more than 2 years conducting hatchery spawning trials and did one of the only controlled experimental outplantings of swimming pāua larvae in New Zealand. Several outplanting methods were tested *in situ* and assessed with follow-up surveys after 3 months. Most of the methods tested did not result in a detectable increase in small recruits in the immediate outplant area. However, one method we trialled, the outplanting of small rocks pre-settled with larvae, showed some promise as a practical and scalable enhancement method. We believe this method may be the most cost-effective of those trialled, and is worth pursuing. Our work highlights the challenges and pitfalls of culturing pāua larvae and outplanting them to the field, and offers practical solutions to the commonest failure points.

This research program has produced informative long-term data sets of commercial enhancement efforts that will help improve site selection and methods for future work. It also provides the details necessary to assess and model likely costs and benefits, which will allow users a way of making more informed decisions about population enhancement. Our results from experimental larval outplanting highlight the challenges and limitations of larval work, and offer an alternative method to mitigate them. Additionally, we offer a practical "how-to" guide of two enhancement methods, compiling insight gained from over 4 years of in-depth research. We trust this will serve as a useful tool to optimise future investments in New Zealand's pāua fishery.

1. Introduction

The global collapse of abalone fisheries over the last century has been widespread and well-documented (Cook, 2016, 2019; Hobday et al., 2000; Karpov et al., 2000; Prince & del Próo, 1993; Raemaekers et al., 2011; Searcy-Bernal et al., 2010; Sloan, 2004; Uchino et al., 2004). With wild stocks in decline many countries are now turning to alternative means of production such as aquaculture, ocean ranching, and heavily subsidised "put and take" fisheries (James et al., 2007; Masuda & Tsukamoto, 1998; Zhang et al., 2004). Indeed, the 2017 closure of the world's foremost abalone fishery in California, USA, proved that even supposedly inexhaustible stocks are vulnerable to collapse (Karpov et al., 2000). Typically, the collapse of abalone populations begins with a prolonged period of overharvesting and serial depletion. Depleted populations then become more susceptible to compounding stressors like disease, environmental change, and natural disturbances (Altstatt et al., 1996; Hobday et al., 2000; Lafferty & Kuris, 1993; McShane, 1995; Shepherd et al., 1998; Uchino et al., 2004).

In response to depletion of abalone populations or as a preventative measure, many countries have invested in various forms of stock enhancement. A common enhancement practice is the outplanting of juvenile abalone (i.e., seed) generated from induced spawning of broodstock and reared for varying time periods in specialised facilities. Outplanting of seed abalone into the wild, commonly referred to as "reseeding", has been done in response to natural disaster mortality, to replenish overharvested areas (Hart, Strain, Fabris, et al., 2013; Kojima, 1995), to re-establish extirpated or functionally extinct species (Rogers-

Bennett et al., 2016), and to supplement harvests (i.e., “put and take” fisheries) (Cook, 2023). Various other enhancement methods have been developed, including larval outplanting, which is the release of competent (ready to settle) swimming larvae instead of settled juveniles. This reduces the rearing time of offspring in the hatchery (days instead of months or years), and increases the number of outplanted individuals exponentially (millions instead of thousands), reducing the cost per outplanted individual. However, despite widespread implementation of these practices in many countries, it remains unclear whether these efforts are having the desired effects or if they are economically viable. In New Zealand, ouptlanting of abalone has received relatively little scientific research despite ongoing implementation and investment.

New Zealand has one of the few remaining wild abalone fisheries in the world, but it is subject to increasing fishing pressure and ongoing concerns about widespread declines. New Zealand blackfoot abalone or pāua (*Haliotis iris*) is the main target of this fishery, which is comprised of cultural, commercial, and recreational fishers. Pāua are considered taonga (treasured) species to Māori, serving as an important food source and cultural keystone (McCarthy et al., 2014; Smith, 2013; Wehi et al., 2013). Compared to other abalone species, adult pāua are shallow-dwelling, with populations generally confined to depths of 1-8 m along inshore rocky reefs (Aguirre & McNaught, 2012; Hooker et al., 1997). Juvenile pāua occupy the low intertidal and shallow subtidal rocky reefs that have abundant coralline algae and cryptic spaces under boulders for predator avoidance. These attributes, and their sedentary nature, make pāua particularly susceptible to shore-based overharvesting and coastal disturbances (e.g., silt and gravel deposition, freshwater flooding, marine heatwaves, and seismic uplift).

Relative to most other countries, New Zealand’s abalone fishery is performing well, with stable commercial catches in the more productive management areas, and customary and recreational fishers readily able to harvest legal daily limits. The commercial sector, which has invested heavily in science and implemented voluntary management initiatives (e.g., larger minimum harvest sizes, finer spatial management and quota shelving) has maintained healthy fisheries across most pāua management areas. Nevertheless, there is increasing concern for the mid- and long-term sustainability of the pāua fishery, which now faces all the usual threats that have caused the collapse of stocks elsewhere. As New Zealand’s population grows, recreational shore-based fishing has become unsustainable, with inadequate regulations allowing harvests many times greater than what has been allocated, causing rapid depletion of accessible stocks (Holdsworth, 2022; Orchard et al., 2023. Schiel et al., 2023) One of the larger commercial management areas (Pau7 – Marlborough Sounds) is rebuilding from historical depletion and facing a “knife-edge” fishery (where most pāua beyond the minimum harvesting size have been fished), as well as environmental stressors. Disturbance events such as storms, coastal erosion, frequent marine heatwaves, and cataclysmic events have caused sudden and extensive pāua mortality and losses of critical habitats and ecological infrastructure (Alestra et al., 2019; Gerrity et al., 2020; Orchard et al., 2021; Schiel et al., 2016; Schiel et al., 2021; Thomsen et al., 2019). Much is being done, largely at the expense of the commercial sector and by fisheries managers, to improve the resilience and sustainability of New Zealand’s pāua fishery. Aside from necessary changes to management practices, commercial stock enhancement is being explored.

1.1 Stock Enhancement in New Zealand

Pāua juvenile outplanting and larval outplanting in New Zealand dates back to the 1980s (Booth & Cox, 2003; Tong et al., 1987). Commercial ouptlanting of hatchery pāua has occurred in most management areas to improve productivity of local fisheries (Roberts et al., 2007). Anecdotal accounts of larval outplanting by commercial divers describe large increases in pāua recruits as a result, although there are no data to support these claims. Despite continual implementation of outplanting practices since the 1980s, surprisingly few studies have quantified the effect of seed pāua on local populations. Schiel (1993) followed seed pāua in the Chatham Islands and Torrey Channel, respectively, and found that survival and growth was highly variable across sites, but that a positive financial return was likely at some sites (Roberts et al., 2007; Schiel, 1993). Roberts et al. (2007) found that outplanted pāua seed in Torrey Channel had highly variable growth and survival, but calculated a positive financial return. Keys (2005) determined the optimal seed size and density for outplanting operations and trialled small constructed boulder reefs to enhance early survival of seed. Tong & Moss (1986) found promising increases in recruit pāua from experimental larval releases around Wellington, but noted that further work was needed (Moss & Tong, 1992; Tong et al., 1987).

Considering the value of the commercial, customary and recreational pāua fisheries, and the widely perceived need for stock enhancement, surprisingly little information is available to those conducting commercial-scale reseeding or larval outplanting. Current commercial implementation of these practices and methods is based primarily on limited field studies from two studies (Schiel, 1993; Roberts, 2007). This present study provides an opportunity to develop tools and improve the sustainability of New Zealand’s iconic pāua fishery.

1.2 Study Background

The impetus for the commercial reseeding that prompted this research was the November 14th 2016 7.8mW Kaikōura earthquake, which caused extensive damage to the nearshore marine environment along c. 130 km of highly productive coastline (Schiel et al., 2016). The earthquake resulted in significant coastal uplift, ranging from 0.1 – 6.4 m, and widespread mortality of algal and invertebrate communities (Clark et al., 2017; Hamling et al., 2017). The effects on the local pāua population were catastrophic, with very high mortality of both adult and juvenile pāua and permanent loss of critical juvenile habitats. An emergency closure to all commercial and recreational harvest was in place from 2016-2021. This resulted in an estimated $14 million revenue loss by the commercial fishing sector and additional local economic losses from a lack of tourism and recreational fishing (Schiel et al., 2019), T. McCowan personal communication).

Sensing a serious threat to their livelihood, the commercial fishing management group PauMAC3 initiated an enhancement program to help restore the population and speed recovery of the fishery. This effort, funded by the Ministry of Primary Industries' Kaikōura Earthquake Relief Fund, commissioned the production and outplanting of 167,000 pāua seed. Larvae were produced from wild-collected Kaikōura broodstock at the Arapawa Seafarms hatchery in Marlborough and reared for 9 months to reach outplanting size (c. 12 mm shell length). Between May-August 2018, the seed were released by hand into juvenile habitat across 5 sites along the earthquake-affected Kaikōura coastline and 1 site near Akaroa on Banks Peninsula (which is c. 270 km south of Kaikōura sites, and outside the earthquake-affected area). PāuaMAC3 was unable to conduct follow-up surveys to measure effects from the reseeding. We proposed a monitoring program intended to gather basic but essential information to inform future reseeding events. In the process of engaging with commercial stakeholders and scientists, we learned of considerable interest in developing other means of enhancement, especially larval outplanting. With these interests in mind, we designed a research program to answer fundamental questions around common enhancement work, with the broad objectives outlined below.

1.3 Research Objectives

Optimise pāua restoration/stock-enhancement efforts by;

A) Assessing commercial reseeding - Does it work? When and how should it be done?

B) Developing stock-enhancement methods - How can we improve outplanting methods and recipient site selection? Does larval outplanting result in numerous pāua recruits settling into the target area? If so, how best do we conduct it and is it feasible? The primary focus of this study was to collect field data on the growth and abundance of the 167,000 hatchery seed pāua released in 2018 by PāuaMAC3, and to assess habitat quality at recipient sites. These surveys extended to a reseeding event that would occur at one additional site in 2020. The secondary focus was to develop techniques for larval outplanting, and conduct an experimental outplanting of larvae with field surveys to quantify survival and growth. Additional work comparing hatchery and wild pāua and different tagging techniques was also conducted and will be summarized in the Appendix.

2. Methods

2.1 Field Surveys of 2018 Commercial Reseeding

2.1.1 Site Selection and seeding

Recipient sites for the initial 2018 reseeding were selected by PāuaMAC3 members based on their experience in fishing along this coastline. They chose areas that had high pāua mortality from the earthquake, but still had intact juvenile habitat (i.e., small boulder fields). Selected sites were Paparoa North, Paparoa South, Lyell Creek, Kaikōura Peninsula, Omihi, and Akaroa (Fig. 1). Note that Akaroa was not affected by the earthquake. Recipient sites were adjacent to subtidal rocky reefs that supported adult pāua, but were underperforming in fishery production prior to the earthquake. Seed pāua were produced by Arapawa

Seafarms Ltd. in the Marlborough Sounds using broodstock collected from the Kaikōura region. A total of 167,000 seed paua were reared in the hatchery over 9 months. At this time, average shell lengths were 12.20.13 mm (mean ± SE) and each seed pāua cost NZ$0.80. Six sites were selected and in May-June 2018 each was seeded with between 8,000 - 50,000 pāua (Fig. 1). At each site, seed were released along a 50-200 m transect at low tide and placed by hand under rocks and into crevices in the shallow subtidal zone. The locations of seeded transects were recorded using GPS and marked with permanent tags for future sampling. Another 4,000 pāua seed were also released at Waipapa in August 2020 because this site had good quality habitat and a low density of resident wild pāua.

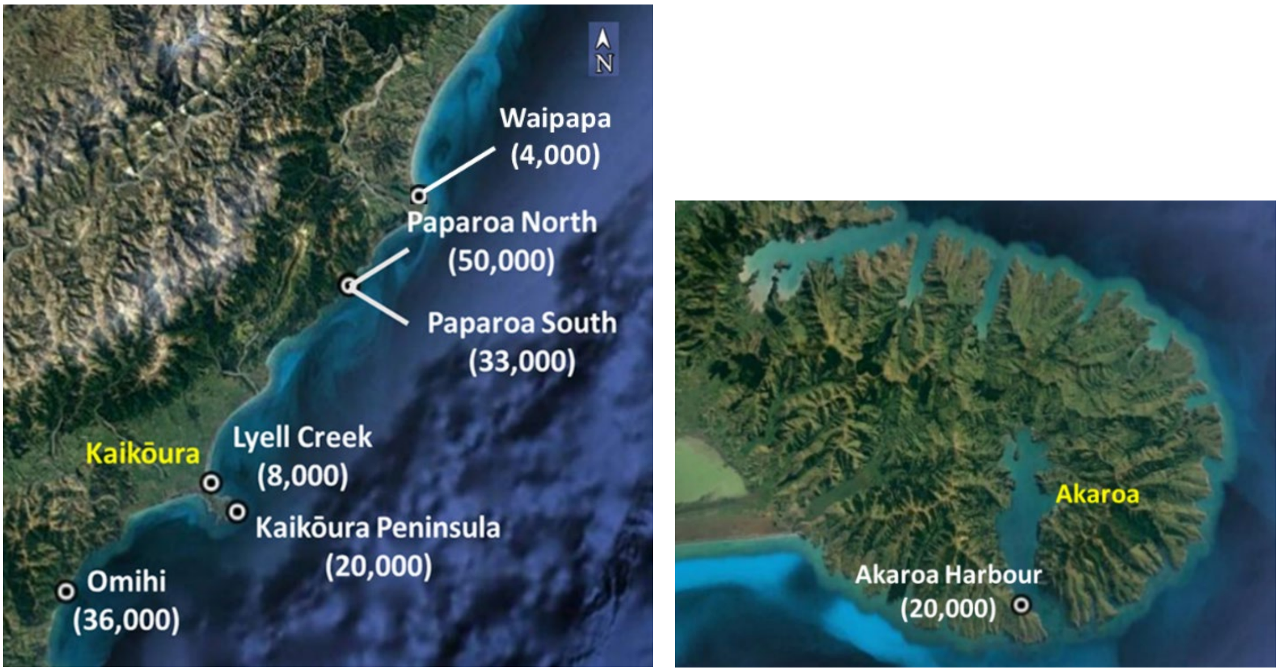

Figure 1. Locations of six sites that were seeded with hatchery-reared pāua in mid-2018, and one site seeded in 2020 (Waipapa), and the approximate number of seed (in parentheses) placed into juvenile habitats. All sites were surveyed annually for seed growth and abundance.

2.1.2 Field Surveys

Quadrat sampling was done to quantify the abundance and size structure of wild and seed pāua, and to assess habitat quality. Sampling methodology was derived from concurrent research assessing impacts of the 2016 Kaikōura earthquake (Alestra et al 2019, Gerrity 2020). At each site, twenty 1 m^2 quadrats were placed along the seeded transect. Within each quadrat all seed and wild pāua were counted and measured using Vernier calipers (Fig. 2). Seed pāua were visually identified by their distinctive blue hatchery cap (Fig. 3). While some wild pāua have blue colorations, the aqua-blue cap of seed pāua can be accurately differentiated with practice. As part of our wider pāua research program we assessed over 30,000 juvenile pāua at 26 non-enhanced sites, none of which had the particular appearance of hatchery seed pāua. Growth rates were estimated by subtracting total shell length from the length of the original hatchery shell cap (Fig. 3). Growth rates were adjusted to annual growth rates using days-at-liberty (the total days between the initial seeding of the pāua and the recapture date).

Percent cover of important habitat features were also recorded, including macroalgae, crustose coralline algae (CCA), silt, gravel, bedrock, and small (125−1,000 cm^3), medium (1,000−10,000 cm^3), and large (>10,000 cm^3) rocks. Surveys were done annually during winter for 4 years after initial seeding. Note that the Akaroa site could not be surveyed in 2022 due to poor ocean conditions. In 2022, 30-minute timed searches with mask and snorkel were done in the subtidal habitats adjacent to the seeded transects at each site to detect outward migration of now mature seed. After 4 years, however, seed pāua were no longer distinguishable from wild pāua, and none were positively identified.

Figure. 2 Left Jason Ruawai conducting surveys of pāua populations at Akaroa one year after commercial seeding; **Right.** A dense patch of juvenile pāua including wild and hatchery seed pāua, the latter indicated with red dots.

Figure 3. **Left.** A tagged hatchery seed pāua recaptured approximately 1 month after release (15 mm in length), displaying red-coloured shell material deposited since release into the natural environment**; Right.** Recaptured seed pāua 6 months after release with distinct blue hatchery “cap”, with red bars showing original hatchery shell length (15 mm) and current shell length (35 mm), from which individual annual growth rates are calculated.

2.2 Larval Outplanting

2.2.1 Production of Larvae

Between 2020 and 2022 we did over 40 pāua spawning attempts in Kaikōura using either some of the 120 broodstock kept in the local pāua hatchery or wild pāua collected throughout the year. Spawning was induced by the hydrogen peroxide method, and fertilisation followed published protocols (Leighton & Robinson, 2008; Moss et al., 1995). Equal numbers of males and females were used in each spawning trial, but spawning success was infrequent due to poor gonad development in the captive broodstock. Unfortunately, we only had 3 successful spawning events, and none produced adequate numbers of surviving larvae for outplanting. To improve our chances of getting competent larvae, we moved our larval experiments to the Arapawa Seafarms Hatchery in 2022. This facility had many broodstock to choose from and a commercial-grade seawater system. However, this meant that any outplanted larvae had to be released locally, and not in Kaikōura, due to biosecurity concerns.

In November of 2022, we successfully facilitated a prolific spawning event and fertilisation at the Arapawa hatchery (Fig. 4). Larvae were observed daily using a microscope to assess settlement competency, which was clearly indicated by the development of a rudimentary foot and exploratory settlement behaviour (Fig. 5). When the majority of larvae (70% based on observations of 100 individuals) were competent to settle, the overall density of the larvae was calculated using 20 sub-sampled aliquots and extrapolating to the known volume of larval solution. At this stage an estimated 410,000 viable swimming larvae were present. Larvae were competent to settle after 10 days.

Approximately half of the larvae were then evenly distributed between 2 “V-tanks”, which are specially designed settlement tanks for commercial rearing of pearl pāua. These larvae were cultured for 9 months at Arapawa Seafarms and their survival and growth rates were recorded 1 month and 10 months post-settlement to serve as a baseline for survival under optimal conditions. The remaining larvae were used for experimental outplanting work.

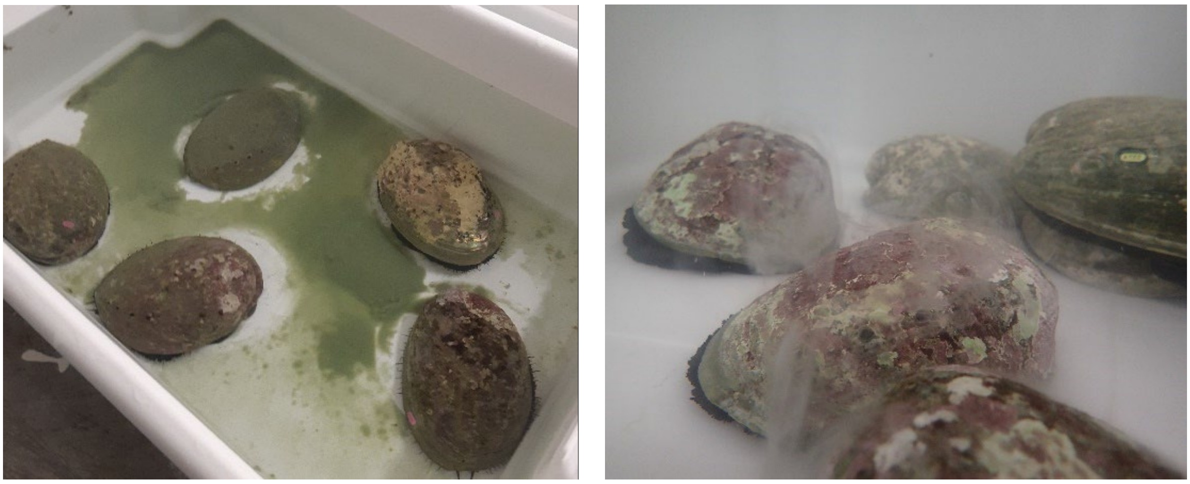

Figure 4 Left. Pāua eggs. **Right.** Sperm release at the Arapawa Seafarms Ltd. hatchery in November 2022.

Figure 5. Example of a 9-day old pāua veliger larva (approx. 200 µm shell length) showing morphology and behaviour indicative of competency to settle, with foot extending from the shell opening and attaching to substrate. Note the velum is still present within the shell, and the larvae has the potential to detach from the substrate and move to a new area via the water column. At this stage the larva has not metamorphosed to a fully-settled juvenile pāua, which lacks a velum.

2.2.2 Larval outplanting field experiment

We tested 3 methods of larval outplanting to assess their efficacy and feasibility. Briefly, these were 1) pouring larval solution into natural juvenile habitat along a transect line, 2) application of larvae to marked 1 m^2 plots, some with larvae contained in “tents” through settlement, and 3) outplanting rocks with pre-settled juvenile pāua. Each method is described in detail below.

2.2.3 Site Selection

The site Okukari (Fig. 6) on Arapawa Island was selected for larval outplanting experiments because it was accessible, had good juvenile and adult habitat, and was relatively sheltered from extreme oceanographic conditions. A nearby site (c. 300m away) acted as a control. At each site we quantified habitat variables and wild pāua abundance and size distribution along a 50 m transect that was run parallel to the shoreline. Twenty 1 m^2 quadrats were sampled every 2-3 m along the transect for habitat composition, and all wild pāua (including very small recruits) were counted and measured. Prior to larval outplanting, we collected 50 rocks of varying size and substrate type (bare, algal crust, algal turf, CCA (crustose coralline algae)) from each site to check for the presence of microscopic natural pāua recruits. These rocks were inspected using a dissecting microscope, and no natural (non-hatchery) pāua were detected.

Figure 6. Okukari, where larval outplanting experiments were conducted. This site received c. 190,000 competent swimming larvae to test 3 different methods.

2.2.4 Experimental Treatments

__Method 1: Transect Outplanting__

Approximately 100,000 competent larvae were outplanted at low slack tide along the 50 m transect. Larvae were gently poured from a 20 L bucket and evenly disbursed along the transect (c. 2,000 larvae per linear meter). Prior to release, i*n situ* water temperatures were identical to hatchery temperatures and larvae were visually inspected to ensure they were healthy. After release the treated area was not disturbed. After 170 days the treated site and the untreated controls site were resampled using the quadrat surveys described above.

Method 2: Marked Plots and Larval Enclosure Tents

Six permanent 1 m^2 plots containing good juvenile habitat were established outside of the transect area at the Okukari site and marked with corner bolts. Prior to the addition of larvae, plots were searched for pāua and none were found. Three of the six plots were randomly selected to receive a direct application of c. 15,000 swimming larvae at slack low tide, while the other three received c. 15,000 larvae that were contained within custom-made larval tents (Fig. 7). Larvae enclosure tents were used to contain larvae and optimise settlement into experimental plots (Schiel 1993). They had triangular walls with 75 µm mesh windows to allow water flow, but not allow larvae to escape. Tents were 1.5 m high and their base was a 1 m^2. The base was weighed down via a heavy chain sewn into the fabric. The top of each tent, which extended slightly above the water surface, had a small opening to pour the larvae into. After applying larvae, the top of each tent was sealed tightly with a large cable tie. A buoy was fixed to the top of the tent to keep it upright as the tidal level increased. Tents were left in place for 24 hours before being removed. At the control site, three 1 m^2 marked plots were established and surveyed for pāua, but no larval solution was applied here. After 170 days, plots were deconstructed and all rocks were inspected for juvenile pāua.

Figure 7. Larvae enclosure tents were 1.5 m high with a 1 m^2 square base; the lighter middle square is plankton mesh. These were placed over three 1 m^2 marked plots at the Okukari site, and 15,000 swimming larvae were gently poured in from the top and left for 24 hours to settle, after which tents were removed.

Method 3: Pre-settled Rock Outplanting

Rocks collected at Okukari were inspected for juvenile pāua, rinsed to remove sediment, and submerged in solutions of pāua larvae for later outplanting to the field. Rocks ranged in size from 125−1,000 cm^3 and had a typical cover representative of the area (CCA, coralline turf, bare space, algal film). To encourage larval settlement on the rocks, rocks were placed in a single layer into four 1 m^2 tanks supplied with filtered seawater. Approximately 5,000 competent pāua larvae were then added to each tank, which were allowed to settle for 48 hours (Fig. 8 Left). After 48 hours, subsamples of the rock were inspected via dissecting microscope for settled larvae (Fig. 8 Right) and initial densities of settled larvae were calculated. After 1 week, the banjo filters were removed from tanks and the water flow was increased to improve growth of settled pāua. After 43 days from initial application of larvae, densities and sizes of surviving larvae were calculated from a subsample of all the rocks across tanks using the above methods. All rocks from each tank were then transported to Okukari and outplanted into four marked 1 m^2 plots. The area around each plot was cleared of rocks to deter pāua migration out of the plot. As a procedural control, four additional bins of cleaned rock that were not pre-settled with larvae were placed into marked 1 m^2 quadrats at a nearby site. After 125 days, plots were deconstructed and rocks were removed and inspected for juvenile pāua.

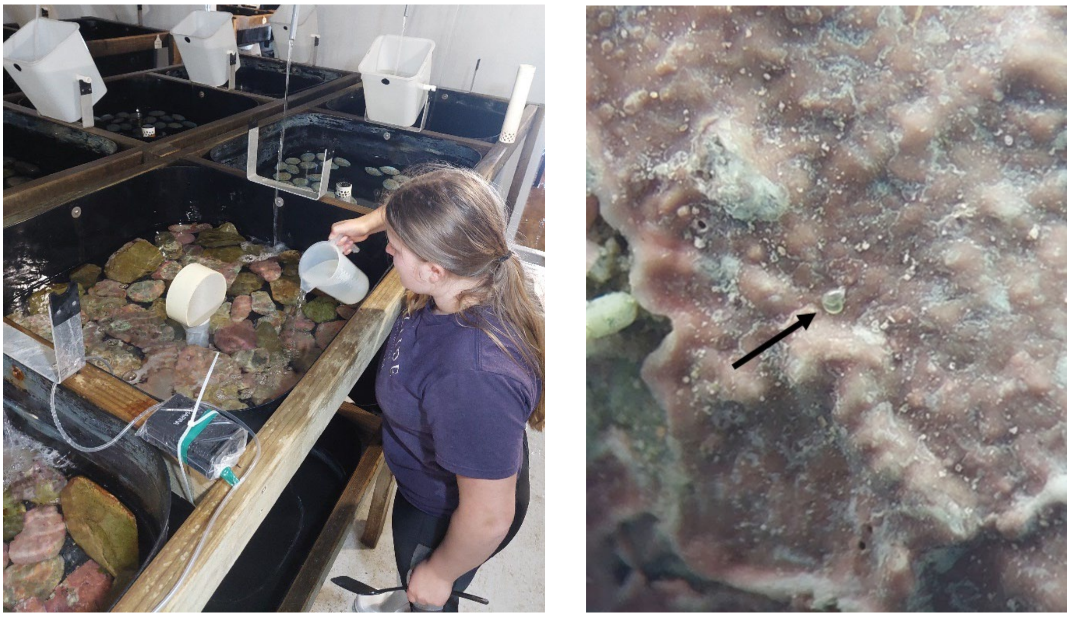

Figure 8 Left. Cleaned ocean rocks were distributed into 4 separate tanks, and each supplied with 5,000 competent pāua larvae; **Right.** After 48 hours, a subsample of rocks was sampled for settled pāua. In this dissecting microscope view (32x magnification), the black arrow points to a pāua of around 0.3 mm shell length.

Table 1 summarises all treatments in the larval outplant experiment, including numbers of replicates and the approximate number of larvae applied to each.

Table 1. Summary of treatments used in larval outplant experiment. A total of 210,000 swimming larvae were used among 4 treatments. Four treatments were tested. A non-treated control site was also used. Larvae were released on 5 November 2023, and pre-settled rocks were deployed on 18 December 2022. All treatments were sampled on 22 April 2023.

Site	Treatment	Larvae applied per replicate (#)	Replicates (#)
Okukari	Transect (50 m)	100,000	1
Okukari	Marked 1m^2 Plot	15,000	3
Okukari	Marked 1m^2 Plot + Tent	15,000	3
Okukari	Pre-Settled Rocks	5,000	4
Control	Transect (50 m)	0	1
Control	Marked 1m^2 Plot	0	3
Control	Rocks with no hatchery settlers	0	4

3. Results

3.1 Field Surveys of Commercial Reseeding

3.1.1 Growth of Outplants

The growth rates of recaptured seed pāua were variable across sites and through time (Table 2) and were much higher than expected over the first year after outplanting, averaging 40 ± 0.60 mm yr^{-1} across the 5 Kaikōura sites. This indicates that outplants were not stunted or shocked by their introduction to the wild. Growth decreased each year (Table 2), which is typical of molluscs that exhibit size-dependent growth. An ANCOVA, with initial shell length as the covariate, confirmed that growth rates decreased significantly each year ($F_{2,823} = 298$, $p < 0.001$).

Table 2. Summary data from commercially reseeded sites surveyed annually from 2019-2022, including total seed released, total seed recaptured (n), months at liberty, average density of seed and wild pāua, average proportion seed pāua in the sampled population, and average growth rate of recaptured seed ± standard error. Note Akaroa was not sampled in 2022. *In 2022 it was not possibly to readily distinguish seed pāua from wild pāua, so values with an asterisk are likely underestimates.

Site (number of seed outplanted)	Sample year	Recap Seed paua (n)	Time at liberty (months)	Mean seed paua (m^{-2})	Mean wild paua (m^{-2})	Proprotion of seed paua in quadrats (%)	Avg. seed growth rate ±SE (mm yr^{-1})
Paparoa North (50,000)	2019	43	11	2.1	6.8	24	39 ± 1.13
	2020	78	24	3.9	11.8	24.8	32 ± 0.36
	2021	37	37	1.8	7.7	19.4	30 ± 0.44
	2022	12*	55	0.6*	4.8	11*	22 ± 0.42
Paparoa South (33,000)	2019	52	12	5.2	7.9	40	44 ± 0.71
	2020	111	26	5.3	19.6	21.3	30 ± 0.44
	2021	28	37	1.3	9.7	11.6	27 ± 0.67
	2022	7*	58	0.4*	15.5	2.2*	21 ± 0.44
Lyell Creek (8,000)	2019	33	12	1.6	18.5	8	28 ± 0.77
	2020	24	24	1.2	43.6	2.7	26 ± 0.72
	2021	14	38	0.6	7.7	7.7	24 ± 0.49
	2022	0*	55	0*	2.6	0*	N/A
KK Peninsula (20,000)	2019	21	11	1.1	4.0	21	45 ± 2.30
	2020	14	25	0.7	4.1	14.6	34 ± 1.42
	2021	13	38	0.6	3.9	14.1	30 ± 0.83
	2022	0*	57	0*	2.3	0*	N/A
Omihi (36,000)	2019	58	11	2.3	9.8	19	43 ± 0.84
	2020	58	24	2.9	13.2	18.0	33 ± 0.52
	2021	28	37	1.2	8.9	11.6	26 ± 0.47
	2022	0*	56	0*	9.1	0*	N/A
Akaroa (20,000)	2019	80	15	3.8	20.4	16	24 ± 0.66
	2020	93	26	4.7	25.8	15.3	19 ± 0.41
	2021	45	38	1.8	16.3	10.0	18 ± 0.62
	2022	N/A	N/A	N/A	N/A	N/A	N/A
All Sites (167,000)	**2019**	**287**	**11-15**	**2.5**	**11.42**	**18**	**36 ± 0.64**
	2020	**381**	**24-26**	**3.1**	**19.7**	**15.9**	**28 ± 0.61**
	2021	**165**	**37-38**	**1.2**	**9.3**	**11.8**	**25 ± 0.46**
	2022	**18***	**55-58**	**0.2***	**6.8**	**2.6***	**21 ± 0.34**
All Sites w/o Akaroa (146,000)	**2019**	**207**	**11-12**	**2.2**	**9.6**	**18.4**	**40 ± 0.60**
	2020	**288**	**24-26**	**2.8**	**17.9**	**13.6**	**31 ± 0.27**
	2021	**120**	**37-38**	**1.1**	**7.7**	**12.6**	**28 ± 0.33**
	2022	**18***	**55-58**	**0.2***	**6.8**	**2.6***	**21 ± 0.34**

After 3 years, outplants at the 5 Kaikōura sites had an average annual growth rate of 25 ± 0.46 mm yr^{-1}(average annual growth calculated from total growth over three years) which is the generally expected growth rate for wild pāua in that region (Table 2)(Naylor & Fu, 2016). Growth was variable across sites, with Akaroa having the slowest growing pāua overall and Lyell Creek having the slowest growing pāua in the Kaikōura region (Fig. 9, ANCOVA $F_{5,823}$ = 298, $p < 0.001$). Pāua growth rates at the other four Kaikōura sites (Paparoa North and South, KK Peninsula and Omihi) were not significantly different from each other. Individual annual growth rates from the 165 seed recaptured at all sites in 2021 show that 55% are growing at ≥ 25 mm yr^{-1} (Fig. 10). All of the 45 recaptured seed from Akaroa were slow growing (≤ 25 mm yr^{-1}). With Akaroa removed, 75% of 120 recaptured seed pāua from the 5 Kaikōura sites grew at ≥ 25 mm yr^{-1} over 3 years. Because Akaroa is not located in the Kaikōura region and has significantly lower growth, it is discussed separately in some instances in this report.

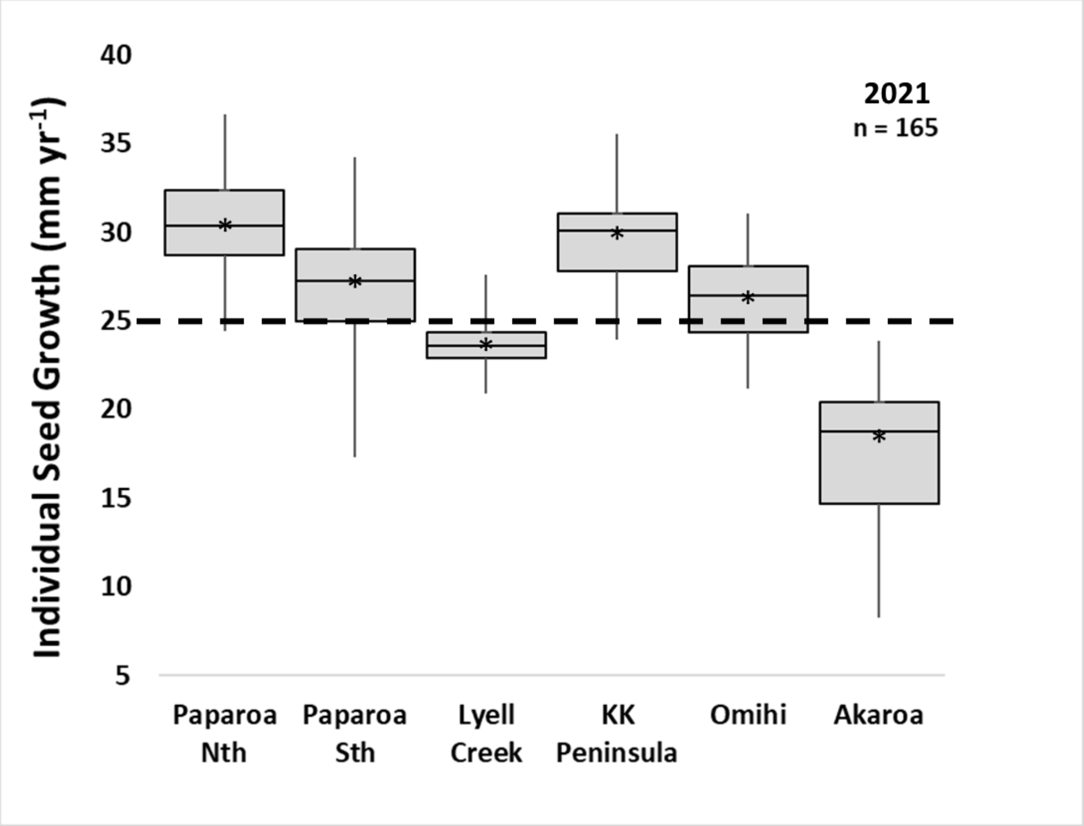

Figure 9. Boxplot depicting annual growth rates of 165 recaptured seed pāua by site after c. 3 years at liberty. Vertical lines indicate the minimum and maximum values at each site and the boxes show the upper and lower quartiles, with a horizontal line to denote the median value and an asterisk for the mean. The dashed line shows the typical annual growth rate for wild pāua in the Kaikōura region. There is a wide range of individual growth rates within and across sites. Akaroa and Lyell Creek showed significantly lower growth rates than the other sites.

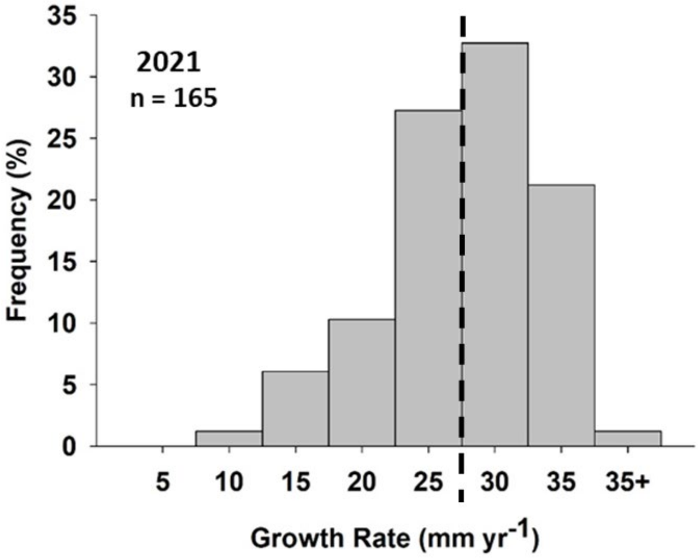

Figure 10. Frequency distribution of individual annual growth rates of 165 recaptured seed pāua in 2021 across all six sites. The X-axis labels indicate the upper bound of each 5 mm size bin, so “25” includes growth rates from 21-25 mm yr^{-1} inclusive. Therefore, everything to the right of the dotted

line has annual growth greater than 25 mm yr^{-1}, which is the typical average annual growth of a wild pāua.

3.1.2 The effect of initial seed length on growth rates

Anecdotal evidence from hatchery managers and researchers who have worked on abalone enhancement suggests seed abalone that are slower growing in the hatchery will remain slow growing once outplanted to field sites, and should be culled (e.g., DR Schiel, previous work). Faster-growing (larger) seed from the same cohort are believed to survive and grow better once outplanted but are more expensive per unit. We tested the effect of initial seed size on growth rate of outplanted seed pāua after 2 and 3 years at liberty, using seed of a range of sizes from the same hatchery cohort. Here we analyse the effect of original shell length (the size of the seed pāua when outplanted in 2018) on individual growth rate in 2020 and 2021 when the effects of "site" on growth rate are already accounted for.

We tested this statistically using an ANOVA of a linear mixed effects model with site as a random effect. This showed that in 2020, when the effects of site on growth rate are already accounted for, the original shell length had a small but significant positive effect on individual growth rate ($F_{1,374.3} = 14.2$ $p = 0.0002$, Figure 11 Top). Using this model, 65% of the variability across all growth rates in 2020 was explained by site and original shell length of seed pāua combined, whereas 2% is explained by original shell length of seed pāua alone ($R^2m = 0.02$, $R^2c = 0.65$). The effect of original shell length was not significant by 2021 ($F_{1,160} = 0.9$ $p = 0.327$, Fig. 11 Bottom), and 67% of the variability across all growth rates is explained by site and original shell length of seed pāua combined, whereas only 0.2% of the variance was due to original shell length of seed pāua ($R^2m = 0.002$, $R^2c = 0.67$). These analyses clearly show that site has the strongest influence on seed pāua growth rates, and that original size of seed has a marginal effect at best, at least over the range of seed sizes used here. This was particularly evident in the poorest performing site, Akaroa, where growth rates were distinctly lower than those of all other sites (Fig. 11).

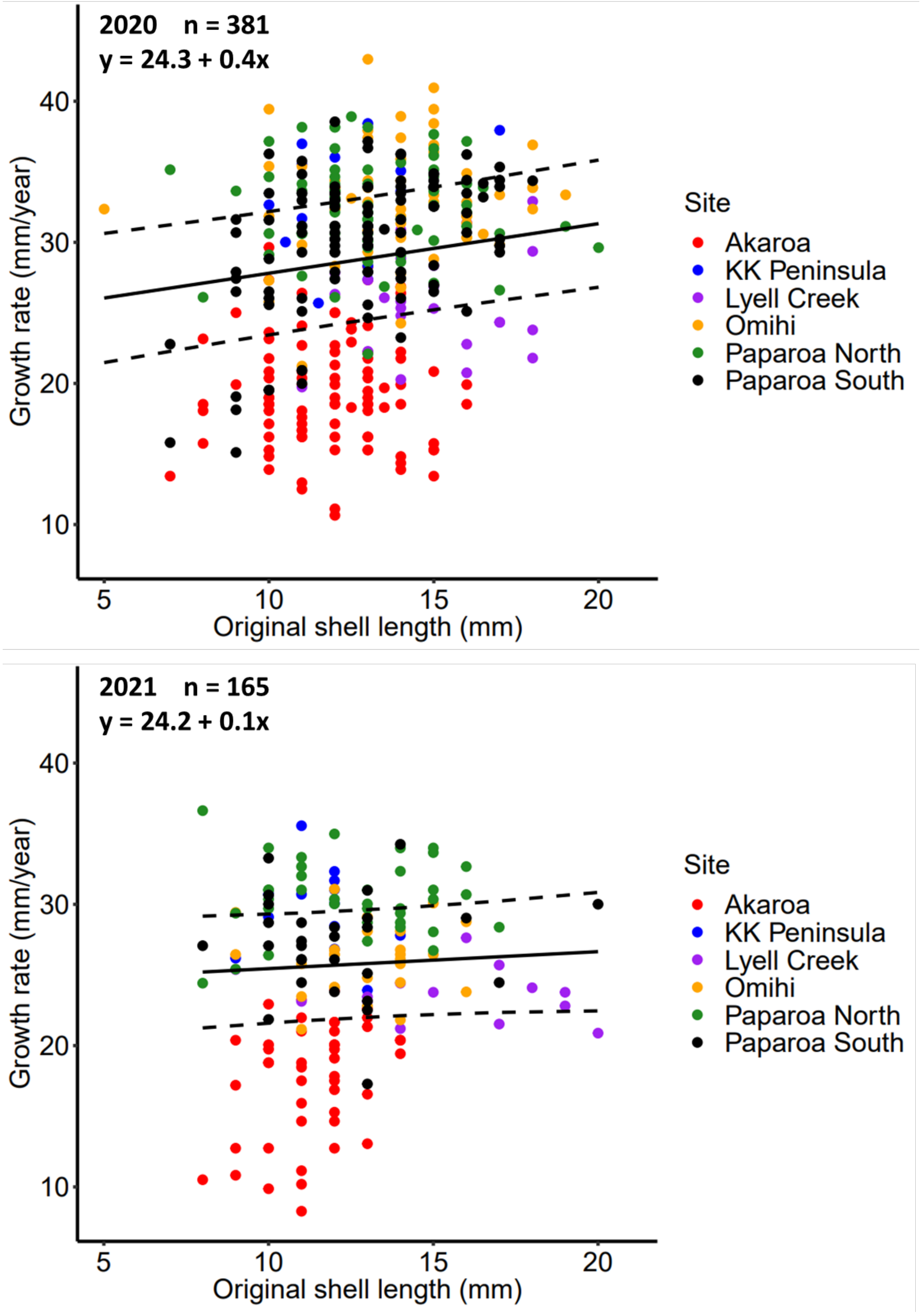

Figure 11. Scatterplot comparing original shell length of seed pāua when they were outplanted in 2018 to their individual annual growth rate after 2 (above) and 3 (below) years at liberty (2020, 2021 respectively), across all sites. The black lines show the mean annual growth rate (mm yr^{-1}) relative to original shell length (mm) and dotted lines indicate 95% confidence intervals.

3.1.3 Size Structure of Outplants Through Time

The distribution of shell lengths of all the recaptured seed over the first three years across the 5 Kaikōura sites shows the progression of seed towards sexual maturity and the fishery (Fig. 12). In 2021 the majority of recaptured seed (96%) had reached the average length at maturity (82 mm) for this region (Naylor et al., 2017). This is the length where 50% of pāua have mature gonads which, although small, will begin to contribute to reproductive output of the population. At c. 102 mm, 95% of the pāua will have mature gonads (Naylor et al., 2017). In 2021, 38% of recapture seed pāua had reached this size or greater. Note that pāua from the Akaroa site are not included here due to poor growth of seed, and geographical dissimilarity. Data from 2022 (all sites) are also not included due to low recapture rates.

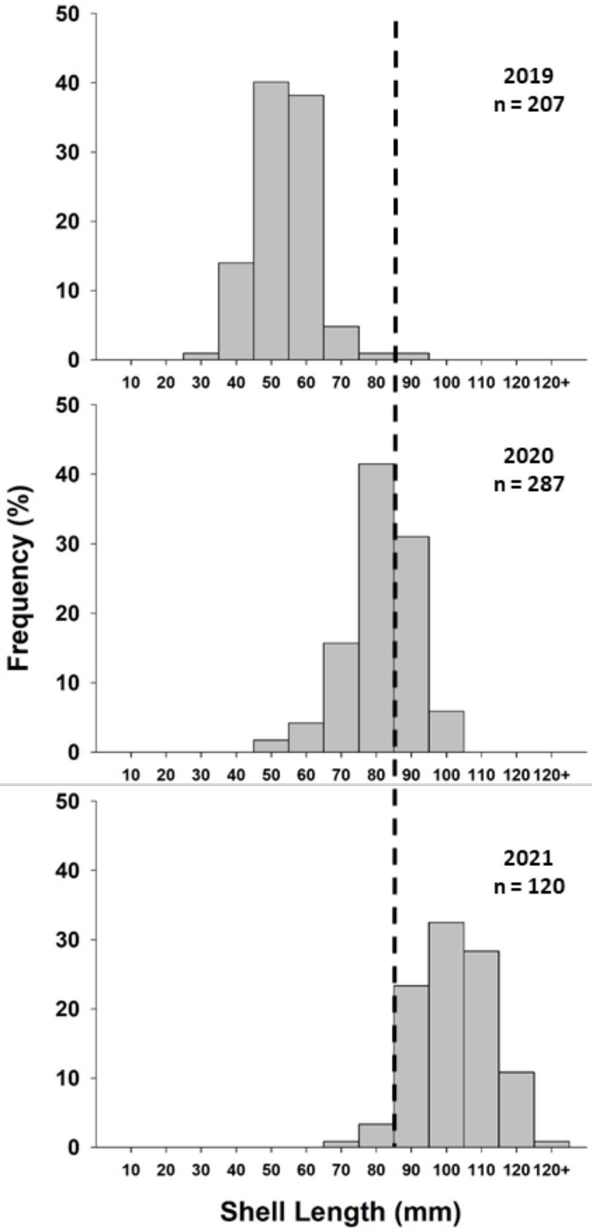

Figure 12. Length-frequency distribution of all recaptured seed pāua, which were outplanted in 2018, across 5 Kaikōura sites for the first 3 years of the study. The X-axis label is the upper limit of the 10 mm size group (e.g., “90” includes all pāua from 81-90 mm). The vertical dashed line represents the approximate length at which 50% of pāua are sexually mature.

3.1.4 Abundance of Seed vs. Wild pāua

The recapture rate of seed pāua was 0.5% of initial seeds, but this does not necessarily indicate poor survival or success. It is not feasible to thoroughly sample 167,000 outplanted pāua spread over thousands of square meters of habitat, many of which are deeply embedded in cracks and under immovable boulders. Therefore, density of seed pāua and wild pāua, and the proportion of seed pāua in the surveyed populations are reported in addition to recapture rates.

The abundances of seed pāua and wild pāua fluctuated by site and through time (Figs. 13, 14). One year after outplanting, across all sites (including Akaroa), 18% (3.1 seed m^{-2} vs 19.7 wild pāua m^{-2}) of all pāua encountered in quadrat surveys were of hatchery origin (Table 2, Fig. 15). In 2021, three years after initial outplanting, seed pāua made up 11.8% (1.2 seed m^{-2} vs. 9.3 wild pāua m^{-2}) of the sampled population (Table 2, Fig. 15). This was despite very high natural recruitment of wild pāua over those years (Fig. 16). Furthermore, there was a positive effect of initial outplanting quantity on recapture numbers, with the sites receiving the most seed pāua in 2018 (Paparoa North and South, Omihi) having significantly greater densities than sites that received fewer seed pāua (e.g., KK Peninsula, Lyell Creek), after 3 years, (ANOVA $F_{1,119} = 10.7$, $p = 0.002$). These are encouraging results and suggest that seed pāua comprise a considerable portion of the overall population at enhanced sites. Four years after outplanting, most seed were indistinguishable from wild pāua, and only 2.8% of the sampled population could be identified as seed.

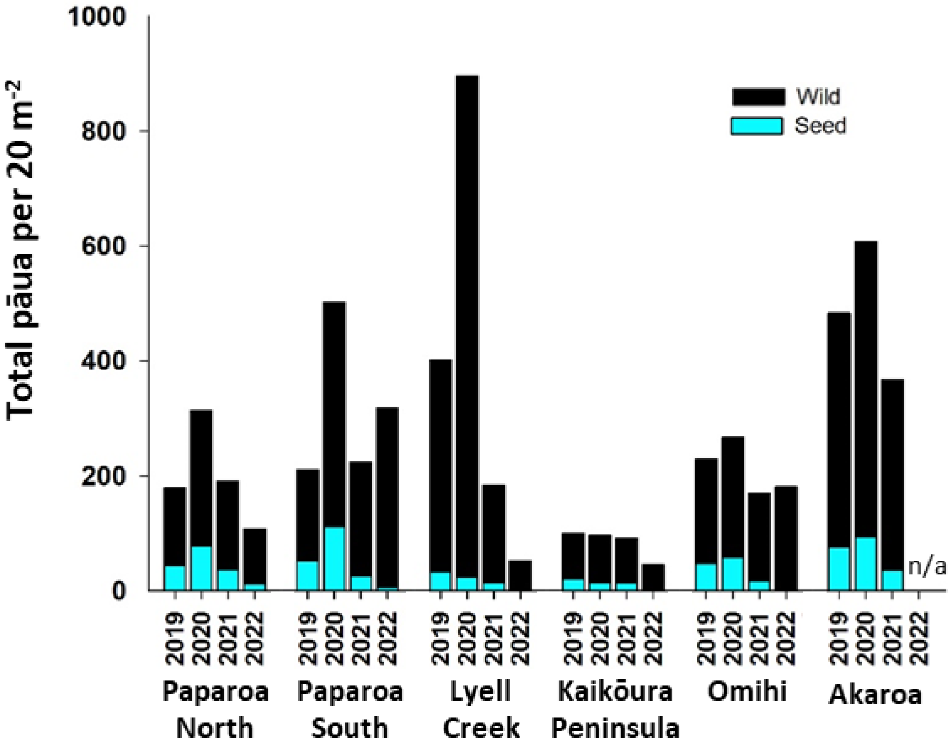

Figure 13. Stacked bar plot showing the annual overall abundance (total count) of seed (blue) and wild (black) pāua across the 20 m^2 of sampled habitat at the 6 sites enhanced with outplanted pāua.

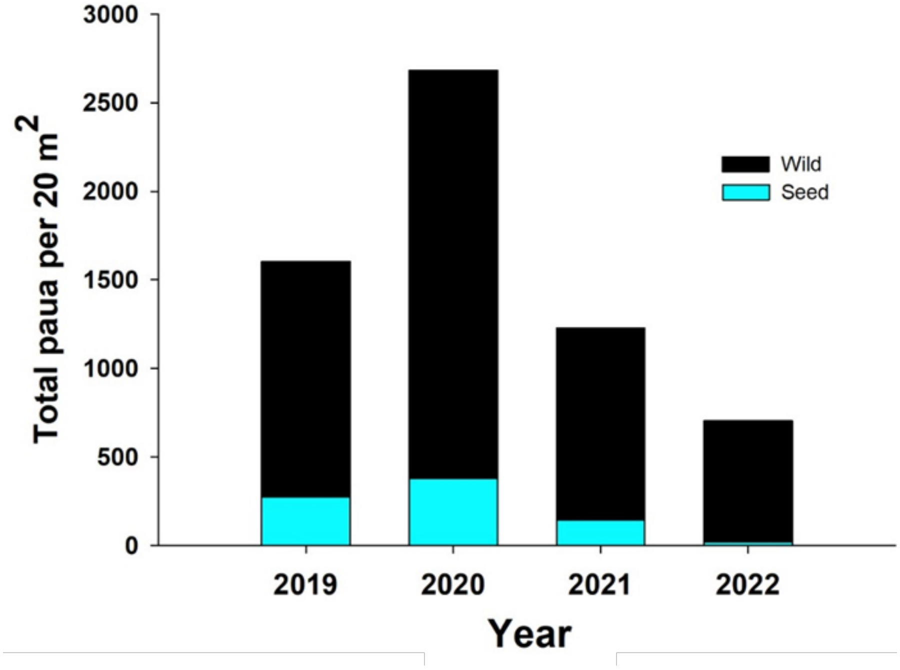

Figure 14. Stacked bar plot showing the annual overall abundance (total count) of seed (blue) and wild (black) pāua across the 20 m^2 of sampled habitat combined across the 6 sites enhanced with outplanted pāua.

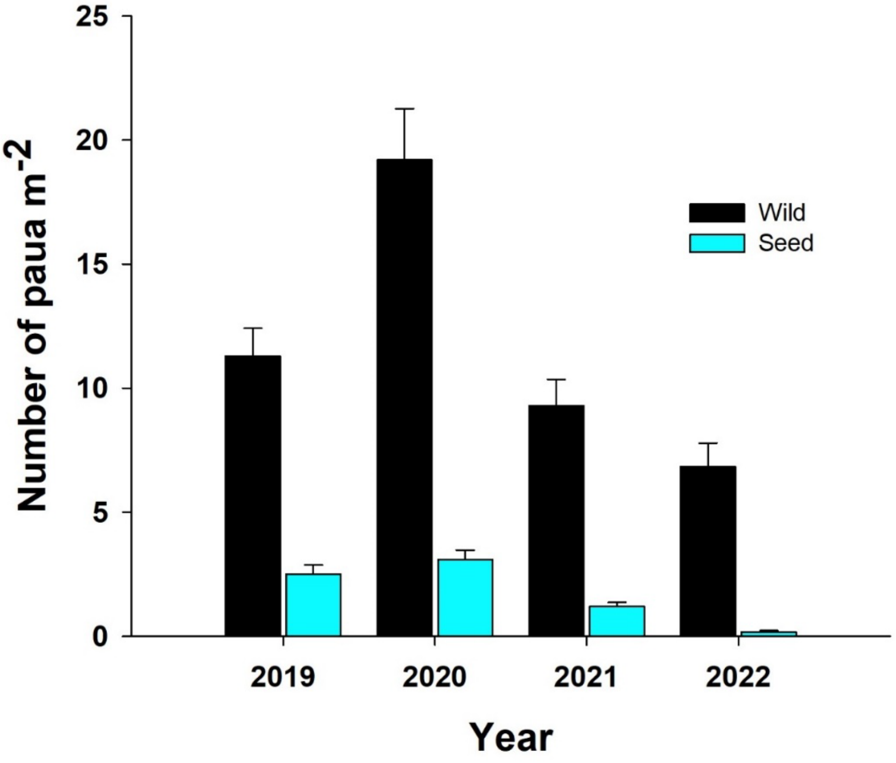

Figure 15. Mean annual density (±SE) of wild (black) and seed (blue) for each year across all 6 sites enhanced with outplanted pāua.

Figure 16. High densities of wild juvenile pāua, here along much of the coast in 2019 and 2020, suggested good reproduction and recruitment within 2 years following the Kaikōura earthquake.

3.1.5 Population Structure at Kaikōura Sites

The size-frequency distribution of pāua (wild and seed) across all Kaikōura sites showed substantial changes in population structure over 3 years (Fig. 17). This is probably due both to the high natural recruitment observed following the earthquake and commercial enhancement of productive sites. In 2022, when seed pāua could not be distinguished from wild pāua, there was a notable increase in 90-110 mm pāua. Many of these could have been of seed origin, but this cannot be quantified without sampling population genetics.

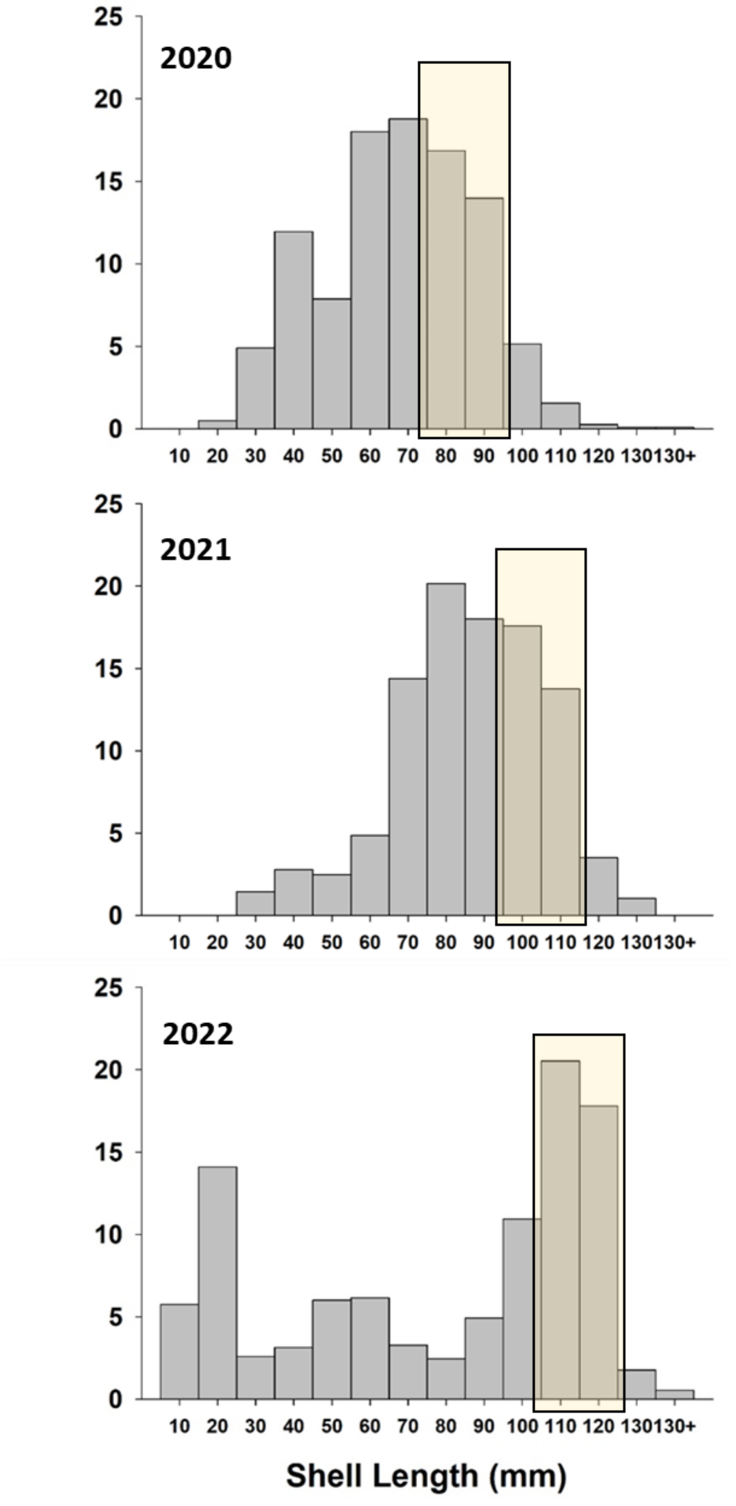

Figure 17. Length-frequency distributions of all pāua measured at all 5 Kaikōura sites in 2019 (top), 2020 (middle) and 2021 (bottom). The yellow box indicates the range of sizes observed in the majority of recaptured seed pāua for each year following outplanting in 2018.

3.1.6 Waipapa Reseeding

Waipapa was selected as an additional recipient site for 4,000 hatchery seed (mean shell length of 13.2 ± 0.2 mm) in August 2020 based on a positive assessment of pāua habitat features of the site (Appendix 1). Seed pāua were released at low tide within a 100 m transect marked with permanent tags (Fig. 18). Surveys were done in November 2021 and July 2023. In 2021, 25 seed were recaptured (0.65% recovery). These seed had an average (± SE) growth rate of 44 ± 0.75 mm yr^{-1}, which is the highest annual growth rate observed in this study (Table 3). Seed pāua comprised 7.8% of the surveyed population and had a mean (± SE) density of 1.2 ± 0.3 m^{-2} (Table 3). However, when the site was re-sampled in July 2023, it had been completely covered by gravel after a severe winter storm (Fig. 19). No pāua were found, but numerous empty shells were observed. This illustrates the importance of spreading enhancement efforts of multiple sites to mitigate the risk of unforeseen, stochastic events.

Figure 18. Waipapa received 4,000 seed pāua in August of 2020 due to its abundance of high-quality habitat and relatively low abundance of wild pāua.

Table 3. Data from two sample events of the Waipapa site (seeded in August 2020), including total seed released, total seed recaptured (n), months at liberty, average density of seed and wild pāua, average proportion seed pāua in the sampled population, and average growth rate of recaptured seed ± standard error. The site was buried in gravel after strong storms in 2023, resulting in high pāua mortality.

Site (number of seed outplanted)	Sample year	Recap Seed paua (n)	Time at liberty (months)	Mean seed paua ± SE (m^{-2})	Mean wild paua ± SE (m^{-2})	Proprotion of seed paua in quadrats (%)	Avg. seed growth rate ±SE (mm yr^{-1})
Waipapa	2021	25	15.5	1.2 ± 0.3	14.1 + 2.0	7.8%	44 ± 0.75
(4,000)	2023	0	35.5	0	0	0	n/a

Figure 19. Waipapa site received 4,000 seed pāua in 2020 (left), but in 2023 was inundated with gravel (right panel) after a cyclone storm. This buried habitats and no living seed or wild pāua were found thereafter, although numerous empty shells were found in the gravel.

3.2 Larval Settlement and Outplanting

Producing larvae for outplanting trials was by far the biggest challenge of this research project. Although the protocols for spawning are straightforward, getting broodstock in spawning condition is a major hurdle. Furthermore, getting male and female pāua to spawn simultaneously was difficult to achieve and, between 2020 and 2022, the vast majority of our 40 spawning attempts were unsuccessful. The adult broodstock kept in the Kaikōura hatchery for 2 years were healthy by all indicators but did not reach peak spawning condition. Over that time we only had 3 successful spawning events, none of which produced enough larvae for meaningful outplanting. This prompted us to move the project to Arapawa Seafarms, which had better facilities and broodstock. It is worth noting that pāua spawning is also highly variable in the wild, and populations can go several years without significant spawning events (Hooker & Creese, 1995; Sainsbury, 1982).

3.2.1 Method 1: Transect Outplanting

The outplanting of 100,000 swimming larvae across a 50 m transect had no detectable effect on the abundance of pāua recruits at Okukari. Surveys 170 days after larval outplanting showed very low abundance of recruit-sized pāua (≤ 15 mm in length), with only 7 recruit pāua found in 20 m^2 of habitat. The average shell length of recruits was 12.3 ± 0.15 mm (Table 4, Fig. 20). We did not find any pāua recruits at the control site, suggesting that the larval outplanting had some effect. However, it is not possible to test for a difference between the control and Okukari sites because the control data was all zeroes.

3.2.2 Method 2: Marked Plots and Larvae Enclosure Tents

Surveys of the 3 marked plots that each received 15,000 swimming larvae without larval enclosure tents had no pāua recruits after 170 days. Similarly, no pāua recruits were found in the three procedural control plots within the control site. In contrast, plots where tents were used to enclose larvae for 24 hours after outplanting contained 11 recruit pāua (density = 3.7 ± 0.67 pāua m^{-2}) (Table 4, Fig. 20). The average shell length of recruits was 11.7 ± 0.72 mm (Table 4). This represents a recapture rate from outplanting of 0.02%.

Table 4. Summary data from larval outplant methods, including treatment, larvae applied per replicate, number of replicates, time at liberty, number of recruits, and mean density and size or recruits.

Site	Treatment	Larvae applied per replicate (#)	Replicates (#)	Time at Liberty (days)	Recruits (≤ 15 mm) paua found	Recruit (< 15 mm) paua density m^{-2}	Mean Size (mm) ± SE
Okukari	Transect (50 m)	100,000	1	170	7	0.35 ± 0.15	**12.3 ± 0.61**
Okukari	Marked 1m^2 Plot	15,000	3	170	0	0	0
Okukari	Marked 1m^2 Plot + Tent	15,000	3	170	11	3.70 ± 0.67	11.7 ± 0.72
Okukari	Pre-Settled Rocks	5,000	4	123	40	10 ± 2.60	6.0 ± 1.7
Control	Transect (50 m)	0	1	170	0	0	n/a
Control	Marked 1m^2 Plot	0	3	170	0	0	n/a
Control	Rocks with no hatchery settlers	0	4	123	0	0	n/a

3.2.3 Method 3: Pre-settled Rock Outplanting

Of the 20,000 larvae placed into tanks and allowed to settle on small rocks, only an estimated 440 made it the outplant stage due to low settlement rates, and poor growth and survival while being held in the hatchery (the density after 43 days was 35 ± 6.24 settlers m^{-2} and the mean shell length was only 0.9 $\underline{+}$ 0.03 mm). It is therefore recommended that future settling of larvae on small rocks should be held in the hatchery for no longer than 7 days prior to outplanting. This should minimise hatchery-based mortality.

A total of 40 recruits ($\leq$ 15 mm) were found within the larval-settled rock plots at Okukari (density = 10 $\underline{+}$ 2.6 pāua m^{-2}), with an average shell length of 6.0 $\underline{+}$ 1.7 mm after 123 days (Table 4, Fig. 20) This was significantly higher ($F_{1,6} = 36.87$, $p = 0.001$) than at the procedural control site, which had only 1 recruit in the four plots that contained rocks that were not pre-settled with pāua. It is worth noting that recapture rates of recruits from larvae was c. 0.2%, whereas recapture rates from settled rocks was 9.1% (Table 4, Fig. 21).

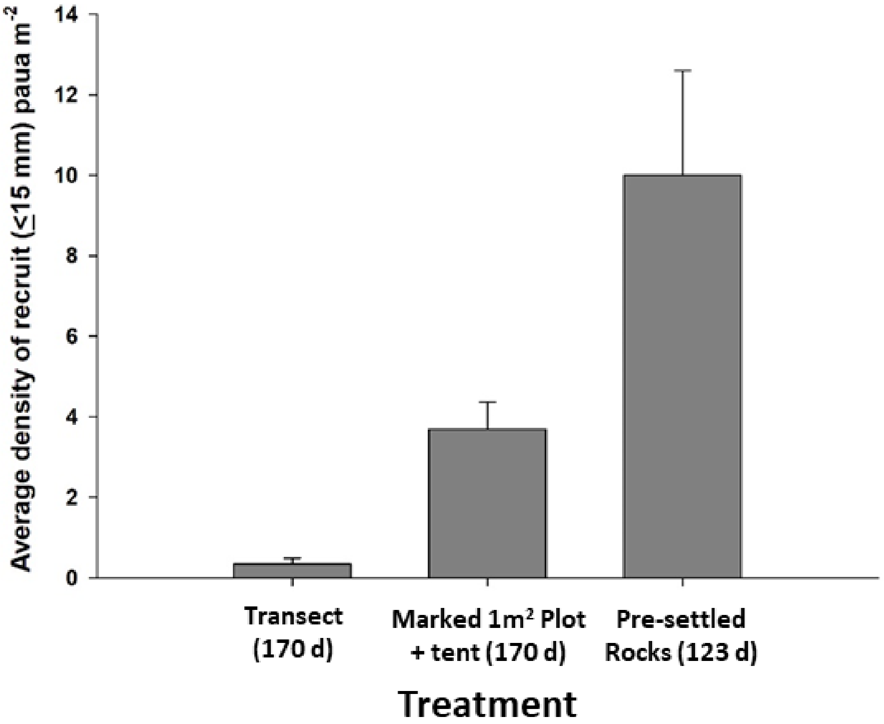

Figure 20. The mean density of pāua recruits ($\leq$ 15 mm in length), resulting from three larval outplanting treatments after 170 and 123 days. No recruits were found in any of the controls, procedural controls, or marked plots without larval tents.

Figure 21. Pāua recruits (<15 mm shell length) were found in patches within pre-settled rock treatment plots (left) but not in most other treatments or any controls. Rocks pre-settled with pāua were placed into marked 1 m^2 quadrats with sand or gravel surrounding them to minimise emigration (right).

3.2.4 Growth and survival of larvae and settlers under hatchery conditions

From the spawning used for larval seeding experiments, many other larvae were used for commercial use in the hatchery. Their growth and survival were used as an indication of performance under optimal conditions to compare with our field-derived results. About 200,000 swimming larvae were settled into two commercial V-tanks with a constant seawater supply and a diatom culture for food. Settled pāua were checked and fed using well-established hatchery techniques for 5 months, which should be conducive to optimal growth and survival. At 43 days post-fertilisation we sampled settler density in the 2 tanks using thirty-five 100 cm^2 quadrats. The average density was 3217 ± 314 pāua m^{-2}, or approximately 40,000 settlers in total. Forty randomly selected settlers were collected from each tank and measured using an ocular micrometer. The average shell length was 1.5 ± 0.12 mm after 43 days. After 5 months, however, there was a sudden mass mortality in both v-tanks. Eleven months (322 days) after settlement, only 538 pāua were still alive. Therefore, the approximate survival rate of pāua from larvae was 0.27% and from settlement was 1.39%, and their average growth rate at 322 days (based on 50 measured individuals) was 25.2 ± 0.7 mm yr^{-1} (Fig. 22). According to the hatchery manager, this sort of die-off is relatively uncommon, and was suspected to be somehow related to contaminated food. It does illustrate, however, the risks that come with prolonged rearing of hatchery pāua. It was interesting to note that these rates were not far off from what we saw in the field.

Figure 22. The 538 surviving hatchery pāua 5 months after the settlement of 200,000 swimming larvae into commercial v-tanks. The average size was 25.2 ± 0.7 mm yr^{-1}.

4. Discussion

The 2016 Kaikōura earthquake was an unprecedented, cataclysmic event that caused extensive destruction and long-term changes to the nearshore environment. At the time, the future of the regional pāua population was uncertain, with high mortality of adults and juveniles and loss of critical habitat along the coast. This was an opportune time to implement a large-scale pāua enhancement programme. The 2018 ouptlanting of hatchery pāua was an attempt to partially offset the losses, and speed recovery of the fishery in the likelihood that reproduction and recruitment were greatly reduced. This also presented an opportunity for collaboration between the commercial sector, the local rūnanga and scientists, so that structured, quantitative data could be generated to inform future enhancement work.

Here we compare the three enhancement methods studied in this program, in the context of our findings and other studies. We then discuss important economic considerations and the various metrics by which to gauge success. Additionally, we offer practical insights gained from this study to help optimise future enhancement work (Appendix 1).

4.1.1 2018 Juvenile Reseeding

Given the severity of the 2016 Kaikōura earthquake disruption to adult populations and juvenile habitats, it was surprising that there was excellent natural reproduction and juvenile recruitment in the 3 years following the earthquake (Gerrity et al., 2020; Gerrity & Schiel, 2023). Despite this prolific influx of natural pāua recruits over the following years, our surveys found a detectible and persistent presence of outplanted seed pāua at all enhanced sites for 3 years after reseeding. By 2021 there was, on average, more than 1 seed pāua per square meter of habitat sampled, and seed pāua composed about 12% of the sample population. This is in line with figures from historical enhancement of commercial abalone fisheries (Hamasaki & Kitada, 2008). At most sites, seed pāua growth was similar or better than growth rates of hatchery outplants from other studies (Roberts et al., 2007). An important milestone was reached 3 years after outplanting, when over half of the seed pāua recaptured were probably sexually mature and contributing to spawning biomass. Despite signs of success at most sites, the poor growth at one site and high mortality due to stochastic events at two other sites emphasised the importance of careful site selection and spreading risk over a wider spatial area if possible. Site selection criteria are detailed in Appendix 1.

Studies from New Zealand and other countries show a wide range of outcomes from experimental and large-scale abalone reseeding programs. Some result in good growth, and survival of outplants ranging anywhere from 2-87% (Dixon et al., 2006; Schiel, 1993; Sweijd et al., 1998), while others show near-total mortality of outplants (Rogers-Bennett & Pearse, 1998; Sweijd et al., 1998; Tegner, 1985). Again, the outcomes seem largely dependent on informed site selection and implementation plans (Roberts et al., 2007; Schiel, 1993; Seki, 2000; Shepherd et al., 2000). The difference between the success and failure of a reseeding, in terms of growth and survival of outplants, can depend on careful planning and a science-informed approach.

Reseeding is one of the more expensive and labour-intensive enhancement methods due to the long hatchery rearing time (Tables 5, 6). However, the results are tangible in real time, and the procedure is spatially targeted. The high habitat fidelity of juvenile outplants allows enhancement of very specific sites, depending on desired outcomes. Examples include a bay that has been overfished, a customary protected area (e.g., rāhui, mātaitai, taiāpure), or sites accessed mostly by commercial fishers. Reseeding is appropriate for areas where juvenile recruitment is poor or interrupted, but where environmental conditions support good growth and long-term survival of outplants. Reseeding is one of the main tools used internationally for enhancement of abalone stocks, but it must be used in conjunction with other management tools, clear goals, and sound harvest strategies.

4.1.2 Larval Outplanting

Our larval outplanting experiments had disappointing results despite a great deal of time and effort. Outplanting 200,000 larvae along transects and in marked plots, even when contained in larval enclosure tents, produced no detectable increase in small pāua recruits after 170 days. We cannot know how many of the larval outplants died, or survived and settled outside of the experimental site. These results could also be a function of larval quantity, and perhaps releases of larvae in the millions would improve outcomes.

Despite the very low cost and perceived advantages of larval outplanting (Tables 5, 6), few studies have shown clear positive effects of this method. Studies of larval outplanting are few and are typically limited to experimental treatments involving great time and effort, which are not commercially scalable and often result in extremely high mortality (Mills-

Orcutt et al., 2020; Preece et al., 1997; Tong et al., 1987). Our results here suggest considerable limitations for this method and a need for further research and development. It should not be assumed that this method is viable until consistent, positive effects can be shown scientifically.

4.1.3 Rock Pre-settled with Larvae

We found encouraging preliminary results from the outplanting of rocks pre-settled with larvae, and a statistically significant positive effect on recruit abundance after 125 days. This method strikes a practical logistical and economic balance between other methods, and shows promise for future development (Tables 5, 6). Perhaps the greatest advantage of pre-settling rock is that it alleviates the critical time constraints imposed by larval settlement. Pre-settled rocks can be kept for days or weeks until logistics and ocean conditions permit outplanting, in contrast to swimming larvae which must be outplanted within a short critical time period (i.e., when they are competent to settle) 10-11 days after fertilisation and are very sensitive to transport and handling techniques. Using pre-settled rocks also has the advantage of being spatially targeted. They can be placed directly into habitats of the target area and will not move, unlike swimming larvae which are nearly impossible to contain within targeted habitats. No published studies have assessed the use of rocks settled with larvae as a means of outplanting, although similar methods have been successfully used for enhancement of kelp (Harger & Neushul, 1983). Interestingly, the use of settled rocks as a method of pāua enhancement was suggested 30 years ago from encouraging results in pilot experiments (Schiel unpublished). It seems appropriate to trial this method on a larger scale.

Table 5: Simple comparison of three stock enhancement methods, including the required rearing time of outplants, cost per 1,000 units, and an estimated proportion of outplants required to reach commercial harvest to recuperate investment.

Method	Rearing Time (days)	Cost per 1,000 Units (NZD)	Proportion to reach commercial harvest to recover cost (%)
Juvenile Reseeding	270	$800.00	7%
Larval Outplanting	10	$1.87	0.02%
Rock Pre-settled with Larvae	15-20	$90.00	1%

Table 6: Summary comparison of three stock enhancement methods, with pros and cons associated with each method described.

Method	Pros	Cons
Reseeding Hatchery Juveniles	Optimizes larval settlement and early growth and survival of settled juveniles	Minimum of 9 months to implement once spawning is achieved - requires daily care from hatchery technician
	Spatially targeted - allows precise enhancement of specific areas and habitats	Expensive at $0.80 per unit (including operating costs and outplanting)
	Initial results are visible and quantifiable - seed paua can be surveyed for up to 3 years to gauge growth	Long rearing time of seed in hatchery (270 days) adds risk of mortality events
	Known and definable recapture rates across an array of sites, allowing the spread of risk	Requires significant effort in manually outplanting seed paua at low tide
Larval Outplanting	Very inexpensive at < $2 per 1,000 units	Larval settlement in natural habitats is unpredictable and not controllable or verifiable
	Does not use hatchery tank space for long periods, so batches can be generated and outplanted continuously as needed	Not spatially targeted - larvae may readily drift out of target area to poor habitat
	Rearing time very short (10 days) - Reduces risks associated with long-term rearing of settled paua in hatchery	Critical time constraint - larvae must be outplanted within 1-2 days from reaching compentency to settle or they will settle in the hatchery - problematic if ocean conditions/weather delay outplanting
	Scalable to commercial volumes - millions of larvae can be released at a time	Difficult to quantify effects without population genetic work or robust controls (surviving juveniles will not be identifiable as hatchery origin)
	Easy to outplant with minimal personnel time in the field	
Rocks Pre-settled with Larvae	Less expensive than reseeding - $90 per 1,000 units	Additional labor costs with transportation of pre-settled rocks
	Critical stage of larval settlement is controlled in hatchery and can be verified	Fairly time-consuming in field as rocks need to be handled with some care
	Spatially targeted - allows precise enhancement of specific areas and habitats	
	Can be held in hatchery for extended time - buys time for ocean conditons to align for field outplanting	

4.2 The Economics of Enhancement

While it is difficult to calculate whether the 2018 commercial reseeding was financially viable, it very likely had positive effects on spawning biomass and the fishery. The purchase of seed pāua and operating costs were $136,000. To recover this directly requires a future commercial harvest of about 4.53 t of original outplanted pāua (c. 11,325 individuals >130 mm, about 6.8% of outplant numbers) or their eventual offspring. Considering that it takes around 7-8 years for most pāua to reach harvest size, a return on investment solely in terms of commercial recovery of outplants will likely be marginal and accrued over a long time period. However, about half of the surviving outplanted pāua were sexually mature within 3 years of release. This signals important, albeit difficult to calculate, returns on investment in terms of enhanced spawning productivity.

Models of the economic benefits of abalone enhancement typically show positive financial returns but which are highly dependent on survival of outplants, cost of seed, market value of abalone meat, and effective fishery management. Studies in New Zealand found that with 10% survival of outplants, a financial return on investment can be 41% (Roberts et al. 2007), although this has some other assumptions. Australian models may be more informative. There, economic models showed that reseeding only covered direct costs if the price of seed was <$0.50 per unit and the market value of abalone was >$25 kg^{-1} (Prince, 2013), and was profitable only if a particular set of harvest control regulations was also in place (Hart, Strain, & Hesp, 2013). This all suggests that many conditions, some difficult to control, must be met for enhancement to achieve profitability.

The economic calculus of pāua enhancement in NZ becomes increasingly complicated, however, when considering that the coast is public domain open to all fishers. Outplanted pāua that reach the minimum legal size (125 mm) are available to recreational and illegal fishers before commercial fishers, who typically fish at larger minimum harvest sizes (130-140 mm). Some sites reseeded in this study are readily accessible by shore-based fishers (Omihi, Lyell Creek, Paparoa N and S), and considering the high habitat fidelity and shallow, sedentary nature of pāua, it is likely that many outplants will remain in accessible habitats as they reach harvestable size. The enormous pressure from shore-based recreational fishers in an area, such as the easily accessible coastline of Kaikōura, could mean that many of the benefits of enhancement are claimed by non-commercial fishers who did not invest in the project (Gerrity & Schiel, 2023). Depending on what outcomes are desired for future enhancement programs, these are important considerations.

4.3 Keeping Clear Goals in Mind

Success of enhancement programs can be gauged in different ways and largely depends on the desired outcomes (Hilborn, 1998; Molony et al., 2003). For example, success in financial terms for the commercial sector might entail a net increase in total allowable commercial catch, or a quota increase over the enhanced area, which would require a sustained increase in the total productivity of the fishery. To achieve this broader outcome, stock enhancement would have to be targeted, large-scale and continual, and require ongoing financial investment. Other positive outcomes may be more achievable over a shorter time span with lesser financial input. For example, reseeding could be used to initiate recovery of a depleted cultural fishery in conjunction with a customary closure such as a rāhui (Bennett-Jones et al., 2022; Gnanalingam, 2013). Enhancement work could also be a success in terms of positive public relations, promoting good resource stewardship and community involvement, or for educational purposes (Prieto-Carolino et al., 2018). These additional benefits should be considered in tandem with strictly financial returns when deciding whether to undertake enhancement work or when calculating cost-benefit scenarios.

5. Conclusion

This work highlights the potential for stock enhancement efforts, and an opportunity to improve current methods and develop novel tools. However, it is important to acknowledge that stock enhancement is by no means a replacement for good fishery management. All of the enhancement methods discussed here are costly both in terms of time and money, and do not guarantee immediate or secure returns. The unpredictability of hatchery abalone spawning limits the response time at which enhancement efforts can be implemented. Juvenile and larval outplanting, if successful, would take a minimum of 6 years to supply pāua into the fishery. Benefits from increased spawning biomass would take much longer to manifest themselves in the fishery. Furthermore, hatchery larval production is inherently low relative to natural spawning. A successful commercial-scale spawning may involve 20 or 30 individuals at best, which is a stark difference to intact natural spawning populations comprised of many tonnes of spawning biomass, or hundreds of thousands of individuals. Therefore, the results from larval outplanting, even if optimised, are far less than what a productive natural spawning population could produce. With numerous examples across global abalone fisheries of the limitations and high costs of stock enhancement and restoration, the greatest priority should be given to the sustainable and conservative management of natural populations.

6. Appendix - Additional Outcomes

6.1 Appendix 1. Optimising Reseeding Efforts and Site Selection

The current methods used by the commercial sector to reseed areas is effective, but improvements can be made. Perhaps the most important metric of success for a reseeding effort, aside from seed survival, is growth rate. To optimize growth means faster advancement to maturity and harvestable size. Slow growing pāua, found mainly at Akaroa, are unlikely to ever reach a harvestable size, representing a substantial loss in investment (Fig. 23). While growth rate for pāua is complicated and variable through space and time, much is known about optimal growth conditions. Water temperature is the primary driver of growth (Naylor 2006), likely due to increased dissolved oxygen capacity, which is also facilitated by wave exposure. Additional considerations like diversity of macroalgae (food) and pāua density are also important (Schiel, 1993). Based on our findings and what is known about pāua growth, we believe there are several ways to optimize growth of outplants;

- Pick recipient sites that have optimal dissolved oxygen levels, which are wave exposed and have consistently cold water. Growth rates for pāua are highest at ~16°C. Exposed sites with colder water should therefore have better growth rates.

- Assess macroalgae abundance and composition (food supply) at recipient sites. Juvenile pāua graze on algal films but eventually require a steady supply of detrital drift algae. Red algae and/or softer brown algae should be present in good abundance.

- Do not introduce seed pāua into areas with high abundances of wild pāua (> 20 pāua m^{-2}). This may cause intraspecific competition for space and food, resulting in reduced seed growth and potentially effecting the growth of the wild stock as well.

- As best as practicable, avoid leaving dense clusters of seed when outplanting. Seed pāua are fairly mobile but it is best to spread them out as much as possible to reduce competition between seed (thus improving growth), minimize large losses by predators, and spread the risk of habitat loss. Avoid leaving large clusters of seed in one area – it is worth the extra time to spread them out (Fig. 24)

Figure 23. Seed pāua recaptured after two years (in 2020) showed a wide range of individual growth rates both within and between sites. Pictured are two seed pāua that were the same initial size (12.5 mm) when released in 2018, recaptured after 2 years in the wild. Left = 35 mm from Akaroa, right = 100 mm from Omihi.

Figure 24. Dense clusters of seed pāua during outplanting. These seed will have high competition with each other for space and food, and be more vulnerable to high predation rates should a predator find them. It is better to spread them at lower densities over a longer transect at each site.

Site selection is very important at ensuring the long-term success of pāua enhancement programs. Investing in preliminary field surveys at potential recipient sites is highly recommended. We have put together an illustrated protocol that can be used to assess the habitat quality and pāua abundance at a given site.

Long-term viability of potential recipient sites should also be considered when possible. Considering that pāua take at least 3 years to reach maturity and 5-8 years to reach harvestable size, recipient sites need to be stable for many years. While most future disasters are not foreseeable, some can be actively avoided. We recommend not enhancing areas adjacent to creek or river mouths, or those surrounded by loose sediment or gravel. Sudden flooding can cause instantaneous loss to the pāua habitat, and large swell can deposit gravel onto intertidal rocky reef (Figs. 19, 25). If possible, consult bathymetric maps to see seafloor composition in the adjacent subtidal area, and avoid sites surrounded with gravel or sand if possible. Finally, because stochastic disturbance events are highly unpredictably by nature, it is best to increase the number of sites to effectively spread the risk over a wider spatial area.

Figure 25. The Lyell Creek Site was one of the best recruitment hotspots along the entire Kaikōura coastline, having high density of wild and seed pāua until it was completely inundated in 2019 by the flooding and gravel deposition from the nearby creek, after which no pāua were found.

6.2 Appendix 2. Additional Outcomes - Habitat Assessments

- Assess the quality and availability of habitat at reseeding sites, and for at least 3 potential recipient sites for reseeding events. Include at least 2 Customary Protected Areas such as rāhui, mātaitai, or taiāpure. Make recommendations to optimise reseeding success and future benefit to fishery.

We have conducted in-depth surveys of habitat and pāua populations of all enhancement sites, as well as 3 additional Customary Protected Areas (Table X). We have a large and detailed set of environmental data and pāua population data that will help inform future enhancement efforts. We are happy to consult with various stakeholders or offer recommendations based on these data.

Table 7. Selected data from in-depth surveys of all sites discussed in this report, and three additional Customary Protected Area sites (in blue).

Site	Avg. Wild Paua Density (paua m^{-2})	Avg. Wave Exposure (1-10)	Avg. Macroalgal Cover (%)	Avg. CCA Cover (%)	Avg. Habitat Complexity (% Cover)	Avg. Sediment Cover (%)	Avg. Gravel Cover (%)	Avg. Predator Density (m^{-2})	Avg. Dead Juvenile Shell Density (m^{-2})
Paparoa North	7.8	4.9	28.0	24.1	79.4	11.3	20.4	0.7	0.2
Paparoa South	13.3	6.0	27.2	43.4	77.2	3.2	5.3	0.4	0.3
Waipapa	9.2	8.5	39.6	30.4	46.1	0.0	19.0	0.0	0.0
Lyell Creek	17.8	5.1	16.6	35.3	67.0	2.3	26.4	0.3	0.4
Kaikoura Peninsula	3.6	6.8	17.4	44.7	74.0	1.5	4.6	0.3	0.2
Omihi	9.5	6.0	34.4	38.4	69.7	5.0	11.7	0.8	0.5
Akaroa	20.1	6.0	8.2	24.1	63.7	0.6	11.2	0.0	0.3
Wairepo taiāpure	5.9	5	14.6	21.3	56.1	9.8	8.7	0.3	0.3
Oaro mātaitai	12.8	5	38.8	30.1	45.3	6.3	6.4	0.1	0.4
Wakatu Quay rāhui	4.7	4	21.5	19.6	34.4	5.3	17.5	0.3	0.2

6.3 Appendix 3. Hatchery vs. Wild Pāua Comparisons

- Conduct experiments to compare growth rate and survival of wild and hatchery pāua either in the field, lab, or both if possible.

We conducted a 1 year *in situ* study comparing the growth rates of tagged wild pāua with outplanted seed pāua over a variety of sites. There was very low recapture rate of tagged wild pāua, and no statistical differences in growth rate or survival could be detected. It did appear that seed growth was faster than wild growth at two sites, although this was inconclusive statistically.

Figure 26. Field pictures depicting various tagged and untagged wild and hatchery seed pāua part of a 1 year study comparing growth and survival.

6.3 Appendix 3. Tagging method comparison

- Evaluate tagging techniques and quantify tag mortality rates using at least two methods of tagging to inform mark-recapture studies for future efforts.

Two tag designs (stick-on vinyl and bee tag), were tested on small seed pāua for retention rates over approximately one year. Two taggers each deployed 50 of each tag onto 100 pāua. Over the course of a year there was found to be better retention of the stick-on vinyl tags, and the bee tags became difficult to read. Tag retention was c. 90% for vinyl tags and only about 65% for bee tags. One tagger had better tag retention than the other, suggesting that tag retention rates can vary by person. Neither tag affected growth rate when compared to untagged control pāua.

Figure 27. Hatchery technician Paul Wolf assisting with experimental tagging and growth studies with seed pāua in the Kaikōura hatchery.

6.4 Appendix 4. Additional Research Outcomes

There has been much interest in this research program over the years, and we initiated much public outreach, science education and scientific communication. A key highlight was working within the Kaikōura community conducting science outreach with local students. We co-developed a program for students at Kaikōura High School around kaitiakitanga, marine stewardship, and pāua biology. Students had to opportunity to come into the field to conduct some release of seed pāua at an experimental site. We received excellent feedback from this project from students and teaching staff, and plan to continue it in the future.

Figure 28. Jason Ruawai and Shawn Gerrity giving lessons to students at Kaikōura Highschool. The theme was about kaitiakitanga, marine stewardship, and pāua biology.

6.5 Oral Presentations

Gerrity S., Schiel D.R. 2023. Cataclysmic mortality, recovery, and reopening of an iconic New Zealand abalone fishery. The 11th International Abalone Symposium. Auckland, New Zealand. 29 February – 2 March

Gerrity S. 2022. Enhancement of New Zealand abalone populations following mass-mortality. Seafood Industry Conference. Nelson, New Zealand. 18-19 August

Gerrity S., Alestra T., Ruawai J., Schiel D.R. 2019. Recovery and restoration of juvenile pāua 2.5 years after the Kaikōura earthquake. New Zealand Marine Sciences Society Conference. Dunedin, New Zealand, 2 - 5 July

Gerrity S., Alestra T., Ruawai J., Schiel D.R. 2019. Recovery of juvenile black-footed pāua (*Haliotis iris*) populations and habitat following the 2016 Kaikōura earthquake. International Temperate Reef Symposium, Hong Kong. 6 – 11 January

Gerrity S., Schiel D.R. 2019. Recovery and restoration of juvenile black-footed pāua (*Haliotis iris*) populations following the 2016 Kaikōura earthquake. Te Korowai o Kaikōura. Community group meeting. Kaikōura, New Zealand.

6.6 Media Coverage

Gerrity S., Yallop A., Schiel D.R. 2019. Giving nature a helping hand. News article, Seafood Magazine. Volume 30 No. 4. August 2019. Pages 6-4.

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