



# Biodiversity associated with restored small-scale mussel habitats has restoration decision implications

Emilee D. Benjamin<sup>1,2</sup>  · Sean J. Handley<sup>2</sup> · Rachel Hale<sup>2</sup> · Trevyn A. Toone<sup>1,2</sup> · Andrew Jeffs<sup>1</sup> · Jenny R. Hillman<sup>1</sup>

Received: 6 March 2022 / Revised: 9 July 2022 / Accepted: 19 July 2022 /

Published online: 6 August 2022

© The Author(s) 2022

## Abstract

The global loss of marine ecosystem engineers has caused an unprecedented decline in biodiversity. Although wild shellfish habitats have been shown to support biodiverse ecosystems, little is known about how biodiversity is altered by restored shellfish habitats, particularly mussels. To explore the biodiversity response to restored mussel habitats we deposited mussels on the seafloor in 1.5 × 1.5 m plots across a gradient of benthic environments. To understand a holistic community response, this study looks at the response of three faunal classifications over 1 year: infauna, epifauna, and pelagic fauna, compared with adjacent control plots (no mussels). The restored mussel habitats recorded 42 times more demersal fish than control areas, while macroalgae and mobile benthic invertebrates had over a twofold increase in abundance. Overall, the addition of mussels to the seafloor resulted in a general reduction of infaunal abundance and biodiversity, but an increase in epifaunal and pelagic faunal abundances, specifically from those species that benefit from benthic habitat complexity and an increase in food availability. From a management perspective, we highlight location-specific differences to consider for future restoration efforts, including environmental conditions and potential observed factors such as nearby sources of species, particularly predators, and relevant demersal fish ranges. Ultimately, measuring biodiversity responses in small-scale studies will serve as a valuable guide for larger scale restoration efforts and this study recommends considerations to enhance biodiversity outcomes in restored mussel habitats.

**Keywords** Green-lipped mussels · Shellfish · Ecosystem services · Epifauna · Macrofauna · Pelagic fauna

---

Communicated by James Tony Lee.

✉ Emilee D. Benjamin  
egol669@aucklanduni.ac.nz

<sup>1</sup> Institute of Marine Science, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand

<sup>2</sup> National Institute of Water and Atmospheric Research, 217 Akersten Street, Port Nelson, Nelson 7010, New Zealand

## Introduction

Marine ecosystem engineers, such as seagrass, coral, kelp, mangroves, and reef-forming shellfish, create biogenic habitat structure that increase biodiversity whilst also providing many other valuable ecosystem services. For example, the habitat provided by shellfish reefs can act as important juvenile fish nurseries (zu Ermgassen et al. 2016; Knoche et al. 2020), stabilise benthic sediments (Commito et al. 2005), reduce water turbidity (Newell 2004), and facilitate nutrient cycling (Ray and Fulweiler 2021; Ray et al. 2021). It is estimated that globally oyster reefs have declined by 85% from their historical extent (Beck et al. 2011), while mussel reefs experienced an overall decline of 53% in Europe, North America, and Australia (Lotze et al. 2006). The widespread decline in these biogenic shellfish populations is likely due to cumulative issues, including overharvesting (Beck et al. 2011), disease (Smith 1985; Beck et al. 2009; Gillies et al. 2018), pollution (Newell 2004), and habitat destruction (Beck et al. 2011). The decline in biogenic shellfish habitat also results in losses of the associated ecosystem services, including the loss of biodiversity, but there can also be wider ecosystem impacts, including trophic disruptions (zu Ermgassen et al. 2006; McLeod et al. 2013; Christianen et al. 2017).

Active human intervention in the form of restoration is increasingly being applied to reinstate biogenic shellfish habitats and with them the ecosystem services they once provided (Coen et al. 2007; zu Ermgassen et al. 2020). However, many studies of the restoration of biogenic shellfish habitats focus on the logistics of restoring the shellfish species without also assessing the ecosystem services provided by the restored shellfish (e.g., Alder et al. 2021; Wilcox et al. 2018; Schotanus et al. 2020; Walles et al. 2016). One key ecosystem service that motivates shellfish restoration efforts is the corresponding increase in biodiversity associated with the restored habitats. However, there is limited understanding of the changes in biodiversity that occurs in these restored habitats (Toone et al. 2021). Scientists have studied biodiversity in wild shellfish habitats and found it to be high compared to adjacent sediment (Commito et al. 2008; McLeod et al. 2013, 2019a). However, biodiversity can depend on many factors, including structural habitat complexity arising from the physical arrangement of shellfish (Grabowski et al. 2005; van der Ouderaa et al. 2021), and aspects of the environment in which the shellfish habitat is located, such as the composition of the underlying benthic sediment (Gray 2002; Commito et al. 2008). For example, the abundance and diversity of both infauna and epifauna in shellfish habitats can be influenced by the grain size profile of the underlying sediment (Commito et al. 2008).

The biodiversity associated with shellfish can be categorized into three distinct ‘faunal classifications’ based on the primary location of occupation within the habitat: infauna, epifauna, and pelagic fauna. Infauna include all organisms living on or in the sediment underlying the shellfish habitat. Epifauna include all organisms, including macroalgae, living on the sediment or on the shellfish, whilst pelagic fauna include all the mobile organisms in the water column above the habitat. These classifications were chosen as they are typically used throughout literature to describe different levels of biodiversity (Willis and Babcock, 2000; Commito et al., 2008; McLeod et al., 2013; Sea et al., 2022). However, there is a tendency for biodiversity studies of shellfish habitats to focus on individual faunal classifications, such as infauna in isolation (e.g., McLeod et al. 2019a, b), pelagic fauna in isolation (e.g., Willis & Babcock 2000), or a combination of epifauna and infauna (e.g., McLeod et al. 2013; Commito et al. 2008). While these studies improve our understanding of the biodiversity found on wild reefs, examining all three faunal classifications is needed to develop a more complete understanding of the overall changes in biodiversity associated

with restoration of shellfish habitats. By understanding biodiversity on restored shellfish habitats, especially at different trophic levels, restoration managers can make informed decisions that can lead to higher ecosystem biodiversity. Additionally, where spatial differences in biodiversity responses can be ascertained, they can be used to greatly improve location selection and overall outcomes from shellfish habitat restoration. This includes targeting important fisheries, maximizing habitat generation, and improving juvenile fish nurseries. In this regard, tracking the response of biodiversity at all three faunal classifications in restored small-scale mussel habitats that are spread across a sediment gradient can be a valuable first step for guiding larger scale restoration efforts.

In New Zealand, the endemic, green-lipped mussel, *Perna canaliculus*, is culturally, economically, and environmentally important (Jeffs et al. 1999). This species forms extensive high-density aggregations, or mussel reefs, on both hard and soft benthic substrata in shallow coastal waters in many parts of the country that used to be up to hundreds of square kilometres in extent (McLeod et al. 2012; Paul 2012). Many of the largest mussel reefs in various parts of New Zealand were fished to functional extinction last century, but the species now forms the basis of a major aquaculture industry (FAO 2021). With a ready supply of aquaculture grown mussels, there is growing community and industry interest in the restoration of the mussel reefs lost through overfishing, and a desire to recover some of the lost ecosystem services from the mussel reefs, including biodiversity. A potential restoration location is Pelorus Sound, an extensive drowned river valley system (~60 km long) which has undergone further ecological changes since the mussels were removed, including increased sediment loads, lower macroalgal abundances, and decreased fish populations (Handley 2015; Urlich and Handley 2020).

To evaluate the effect of shellfish restoration in Pelorus Sound on infaunal, epifaunal, and pelagic faunal biodiversity a series of small-scale experimental restored mussel plots were placed at four locations spatially distributed over ~30 km along Pelorus Sound and subsequent changes in biodiversity of the three faunal classifications were measured over a 1-year period. The four locations included habitats covering a benthic sediment gradient from fine mud to sand and rock. We hypothesised that: (1) the biodiversity observed in the four locations would differ based on the underlying sediment composition (i.e., regardless of mussel addition), and (2) the addition of mussels would alter the benthic environment, increase benthic structural complexity and food availability, and therefore change the structure and abundance of the infaunal, epifaunal, and pelagic faunal communities.

## Methods

### Study location

Pelorus Sound, is located within the Marlborough Sounds on the north-eastern tip of New Zealand's South Island (Fig. 1). Pelorus Sound is a drowned river valley system comprised of multiple arms and bays with a large catchment area, high annual average rainfall, steep topography, and a variety of landuse throughout which leads to regular excessive sediment influxes (Urlich and Handley 2020). This study took place over ~30 km at four coastal locations of 5–7 m depth along a seaward gradient with decreasing clay and silt fractions that are described in the results: Grant Bay (GB), Maori Bay (MB), Skiddaw (SK), and Te Mara (TM). These locations were chosen as they historically supported mussel populations



**Fig. 1** Locations of the four experimental mussel habitats in Pelorus Sound, New Zealand

(Stead 1969; Flaws 1975) and using a drop camera the benthic habitat was assessed to ensure each location composed of bare sediment without any biogenic habitat.

### Restored mussel habitats

At each location six plots of  $1.5 \times 1.5$  m were randomly selected in a 1 ha area and three assigned as restored (mussels added) or a control plot (no mussels added). The experimental plots were deployed in January 2020 by translocating a 256 kg bag of adult, green-lipped mussels (mean shell length =  $91.3 \pm \text{SE } 6.5$  mm) to the seafloor at each plot within 24 h of being harvested from a mussel farm in Grant Bay. The seafloor was not altered prior to the deployment and the mussels were harvested in clumps and deployed at a high density to ensure anchorage with conspecifics on the soft sediment. The density of mussels at deployment within the original  $2.25 \text{ m}^2$  area ( $\sim 2000$  mussels  $\text{m}^{-2}$ ), however mussels have the ability to self-organize and after 1 month the restored mussel plot areas were  $5.7 \pm 0.3 \text{ m}^2$  ( $915 \pm 45$  mussels  $\text{m}^{-2}$ ). The original plan was to perform sampling at 6- and 12-months but due to weather and field logistics they were sampled at 5- and 13-months. The corners of each plot were marked and labelled with steel pegs driven into the sediment. Mussel survival was measured using a method modified from Wilcox et al. (2018), where SCUBA divers randomly placed a  $0.25 \times 0.25$  m quadrat three times in each restored plot, at least 0.5 m from the edge of the plot. The mussels inside the quadrat (where more than 50% of the mussel shell was inside the quadrat), were counted as alive and dead, where either whole shells or two half shells were counted as one dead mussel. The percent survival of

mussels was calculated by taking the proportion of live mussels out of the total of both live and dead mussels recorded for each quadrat. As eleven-armed sea stars, *Coscinasterias muricata*, are a threat to restored mussel survival in New Zealand (Paul-Burke and Burke 2013; Wilcox and Jeffs 2019), they were collected and removed after the deployment, 1, 5- and 13-month sampling events.

### Sediment characteristics

Initial sediment grain size was assessed prior to the mussel deployment using a Ponar grab (scoop area 0.05 m<sup>2</sup>, maximum depth 15 cm) at three points within each location, except for Grant Bay, which was too rocky for the grab and was instead sampled by SCUBA divers using sediment cores to collect interstitial sediment amongst cobbles. Sediment cores (volume 25 ml, maximum depth 6 cm) were collected after the mussels were on the seabed for 5- and 13-months using SCUBA divers to obtain three sediment samples per plot (both control and restored plots). Samples were stored at – 20 °C until analysis. Organic content samples were dried at 60 °C and weighed (D), before combustion at 500 °C for 4 h and reweighed (B) (Parker 1983). Sediment organic content (SOM) was determined using the equation:  $SOM\% = 100(\frac{D-B}{D})$ . To calculate grain size, the samples went through an organic content digestion (6% hydrogen peroxide for 24 h followed by 5% Calgon for 24 h) before particle size determination using laser diffraction (Malvern Mastersizer 3000).

### Biodiversity assessment

In June 2020 (austral winter), 5 months after the mussel deployment, and in February 2021 (austral summer), 13-months after the mussel deployment, the diversity of three faunal classifications: infauna, epifauna, and pelagic fauna, present on the restored mussel plots and the control plots was assessed. Infauna and epifauna were taken at all four mussel deployment locations, but pelagic fauna was assessed at only two locations due to logistical constraints (Table 1). Before assessment of each plot, divers first placed

**Table 1** Number of samples taken at each sampling period per faunal classification by location

Location	5-Months	13-Months
Grant Bay		
Infauna	18	16
Epifauna	6	6
Maori Bay		
Infauna	17	18
Epifauna	6	6
Pelagic	6	6
Skiddaw		
Infauna	17	18
Epifauna	6	5
Pelagic	5	6
Te Mara		
Infauna	15	18
Epifauna	5	5

a square quadrat frame (1.5 × 1.5 m) over the permanently marked to ensure the same location at each sampling period. Due to field logistical constraints and technical difficulties (i.e., camera failure) a few plots were not sampled at each sampling period; the 5-month sampling had 101 samples taken across the three faunal classifications (49% of total samples), while the 13-month sampling had 104 samples (51% of the total samples; Table 1).

## Infauna

To assess the infaunal organisms, PVC pipe sediment cores (volume 1.5 L, depth 17.5 cm) were pushed into the sediment in three randomly placed locations within each plot, avoiding the area 0.5 m from the plot edge. A depth of 17.5 cm was chosen to be comparable with other shellfish studies that sample infauna with cores ranging from 10 to 20 cm (Sea et al 2022; Commito et al. 2008; van der Ouderaa et al. 2021). In the restored plots the mussels were moved from the sediment being cored and then replaced. The core was sieved through a 500 µm mesh bag to remove the sediment, and the retained material preserved in 80% ethanol and stained with Rose Bengal. In the laboratory the samples were sieved to 1 mm, sorted, and the infauna identified to the lowest practical taxonomic group.

## Epifauna

To assess the epifaunal organisms, video transects of both the control and the restored plots were taken using an Olympus TG-5 underwater camera in a waterproof housing with a light attached. A video transect was recorded across the entire plot with the camera staying 25 cm above the seafloor. This method was chosen to ensure cryptic fauna were identified and to maintain the same distance from the seafloor at each location. Each video was reviewed twice independently by two different assessors who identified, counted, and recorded all conspicuous fauna and flora within the mussel and control plots. Barnacles and gastropods were excluded from these analyses due to the difficulty in determining live animals from empty shells in the video recordings.

## Pelagic fauna

To assess the pelagic fauna on the plots, underwater video sampling was used following a method modified from Parsons et al. (2020) at two locations (Skiddaw and Maori Bay). A camera (Go Pro Silver 7 with an extended battery pack, mounted height 40 cm) was mounted facing each plot at 0.5 m and 20 m away from each restored plot as a paired control. The existing control plots that were associated with the restored plots were not used as they were considered too close to the restored plots considering the mobility of the pelagic fauna (Parsons et al. 2020). The first 30 min of each recording were removed due to the potential for interference with fish behaviour from the presence of divers placing the cameras on the seafloor. Each recording was then standardized to 3.5 h duration, to match the shortest recording. Recordings were analysed by two assessors to ensure all mobile fauna were identified and counted from each recording. Each pelagic organism that came into the camera frame was counted as an individual to ensure consistency throughout.

## Statistical analyses

Differences in sediment variables (i.e., grain size, sediment organic matter) were checked for normality and then assessed using three-way repeated measures ANOVAs, with location, the addition of mussels, and sampling period as factors with plot as the repeated measure. Differences in the assemblages of organisms for the three faunal classifications were assessed individually with a distance-based permutational multivariable analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarity measures (Anderson 2001; McArdle and Anderson 2001) using the ‘vegan’ package in R (Oksanen et al. 2020; R Core Team 2021). For each faunal classification, epifauna, pelagic fauna, and infauna, an individual 3-factor PERMANOVA was performed with location, the addition of mussels, and sampling period as the factors. Non-metric multidimensional scaling (nMDS; Kruskal and Wish 1978) ordination models based on Bray–Curtis dissimilarity matrix (Clarke and Green 1988) were used to plot and visualize differences in epifauna and pelagic fauna assemblages individually with location, the addition of mussels, and sampling period as factors. For infauna, the nMDS plot stress was high (stress = 0.23), so a Canonical analysis of principal coordinates (CAP) based on Bray–Curtis similarity was used in PRIMER v7 (Clarke and Gorley 2015). To explore correlations between the infauna taxa and the sediment composition in the mussel versus control plots, Pearson vector overlays were plotted with a correlation threshold of  $P > 0.5$ . Pearson’s chi-squared tests were used to determine differences in infauna taxa counts in the three highest groups. The similarity procedure SIMPER was used to identify taxa that were key contributors to location and treatment differences for the three faunal classifications.

Univariate indices were determined in all faunal classifications individually to describe the taxonomic community of organisms (total abundance, richness (number of taxa), Shannon–Wiener diversity, and Pielou’s evenness) according to location, the addition of mussels, and sampling period. Pielou’s evenness indicates the degree of dominance of a species in a community when a value of 1 represents equal abundance of multiple taxa and a value of 0 indicates a single dominating species or taxon (Pielou 1966). The Shannon–Wiener diversity index is used as a diversity measure that accounts for the abundance and evenness of the taxa present (Heip and Engels 1974). Univariate indices were analysed using linear mixed-effects models (LME) using the R package *lme4* (Bates et al. 2015). In these models, the response variables were the univariate indices (abundance, richness, diversity, or evenness), fixed effects were location, the addition of mussels, and sampling period, and plot number was the random factor. To obtain the p-values of all the fixed effects in the models, the Anova function from the R package *car* was used (Fox and Weisberg 2019). Significance was further examined for each univariate variable using pairwise Wilcoxon tests (“predictmeans” function in R) with a false discovery rate correction for multiple comparisons (“fdr” function in R) to account for the lack of independent replicates over the two sampling periods. Univariate statistics were calculated using R statistical software (v 3.2.3; R Core Team 2021).

## Results

### Mussel survival

Mussel survival was high at three of the four locations at 5-months and 13-months (Maori Bay, MB; Skiddaw, SK; and Te Mara, TM; 5-month mean  $98.0 \pm \text{SD } 2.1\%$ , 13-month mean  $93.6 \pm 4.6\%$ ), while Grant Bay had the lowest survival at both sampling periods (5-month mean  $86.8 \pm 6.8\%$ , 13-month  $60.3 \pm 14.6\%$ ). Visual assessments by divers reported no larval recruitment into the mussel plots.

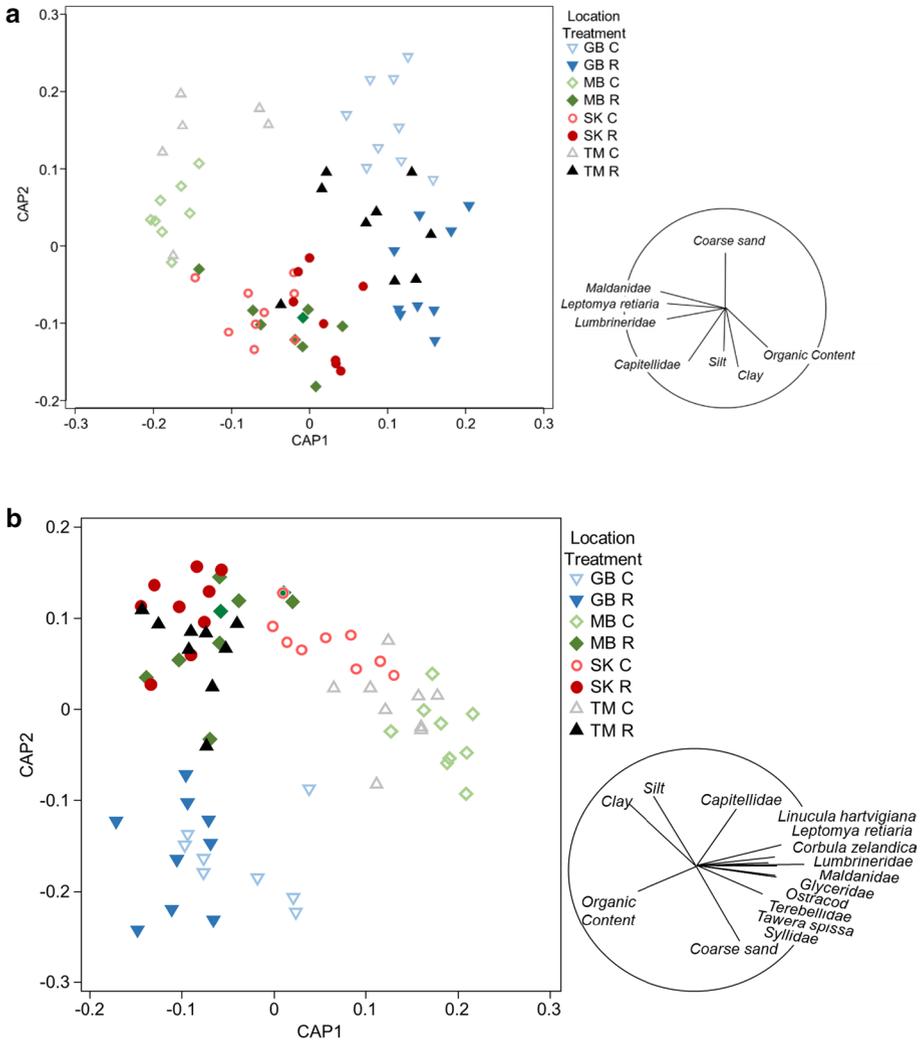
### Sediment characteristics

Benthic sediment characteristics prior to the mussel deployment varied by location along a seaward gradient with decreasing clay and silt fractions in the sediment along Pelorus Sound: GB (47.1% coarse sand), MB (52.2% coarse sand), SK (31.0% silt), and TM (44.6% silt). This pattern was consistent throughout the study with both clay and silt proportions differing by location [3-way ANOVA; silt  $F_{(3,122)} = 105.32$ , clay  $F_{(3,122)} = 27.60$ ; both  $P < 0.001$ ] but did not change between the 5-month and 13-month sampling period [3-way ANOVA; silt  $F_{(1,122)} = 0.54$ , clay  $F_{(1,122)} = 27.60$ ; both  $P > 0.05$ ]. There was a significant interaction between location and the addition of mussels [3-way ANOVA; silt  $F_{(3,122)} = 4.83$ , clay  $F_{(3,122)} = 3.66$ ;  $P < 0.05$ ] indicating that the trends in grain size were not independent for either factor. Overall, the restored plots had 2.1 times higher proportion of clay and 1.7 times higher proportion of silt than the adjacent control plots (mean  $\pm$  SD, restored plots  $16.6 \pm 4.6\%$  clay and  $53.7 \pm 19.2\%$  silt, control plots  $8.1 \pm 2.6\%$  clay and  $31.3 \pm 16.8\%$  silt; while coarse sand ( $> 500 \mu\text{M}$ ) was 2.6 times higher on the control plots versus the restored plots (mean  $\pm$  SD, control  $24.0 \pm 15.9\%$ , restored  $9.2 \pm 10.3\%$ , 3-way ANOVA;  $F_{(1,122)} = 125.80$ ;  $P < 0.001$ ).

Sediment organic content differed by location [3-way ANOVA;  $F_{(3,139)} = 7.20$ ;  $P < 0.001$ ], but did not change between the 5-month and 13-month sampling period [3-way ANOVA;  $F_{(1,139)} = 1.11$ ;  $P > 0.05$ ], and there was a significant interaction effect between the addition of mussels and location [3-way ANOVA;  $F_{(1,139)} = 4.60$ ;  $P < 0.05$ ], where despite having similar organic content in the control plots (mean  $\pm$  SD, SK  $4.2 \pm 1.2\%$ , MB  $4.9 \pm 2.9\%$ , GB  $5.3 \pm 2.6\%$ , TM  $5.6 \pm 1.4\%$ ; Pairwise t-test;  $P > 0.05$ ), Grant Bay (GB) had a higher organic content under the mussel plots than occurred at the other three locations (mean  $\pm$  SD, SK  $7.6 \pm 2.0\%$ , TM  $7.7 \pm 2.0\%$ , MB  $9.0 \pm 2.1\%$ , GB  $11.6 \pm 4.0\%$ ; Pairwise t-test;  $P < 0.05$ ). Overall, the restored plots had a 1.8 times higher organic content than the adjacent control plots [mean restored  $9.0 \pm 3.1\%$ , control  $5.0 \pm 2.2\%$ ; 3-way ANOVA;  $F_{(1,139)} = 97.54$ ;  $P < 0.001$ ; for further details of all ANOVA results see Online Resource 1]. Pearson vector biplots showed these patterns, with organic content, silt, and clay correlating with restored plots and coarse sand correlating with the control plots (Fig. 2).

### Infauna

Over the two sampling periods a total of 1051 invertebrates from 57 different taxa were identified on the restored plots from 71 cores, while the control plots had 3254 invertebrates from 82 taxa from 66 cores (Table 2). The most abundant taxa in both the control and restored plots were polychaetes from 25 different families comprising 62% of the total abundance of identified fauna (69% on restored plots, 59% on control



**Fig. 2** Canonical analysis of principal coordinates (CAP) analysis using Bray–Curtis similarity in **a** 5-months, and **b** 13-months. Restored plots (R) have filled in shapes, while control plots (C) have empty shapes. Locations are abbreviated Grant Bay (GB), Maori Bay (MB), Skiddaw (SK), Te Mara (TM). Vector plots are Pearson correlation for taxa and sediment composition exceeding  $p > 0.5$  are superimposed

plots; for further details of infauna results see Online Resource 2). The most abundant polychaete families were Capitellidae (24.2% on restored plots, 14.1% on control plots), Spionidae (26.4% on restored plots, 8.9% on control plots), and Lumbrineridae (3.2% on restored plots, 10.4% on control plots). The next most abundant taxa were bivalves (12 taxa: 16% on restored plots, 14% on control plots), and crustaceans (5 taxa: 9% on restored plots, 12% on control plots). Three taxonomic groups were recorded in higher abundances on the control plots than the mussel plots: bivalves [2.9 times higher; Chi-squared;  $X^2_{(23,137)} = 46.35, P = 0.003$ ], polychaetes (3.3 times higher;

**Table 2** Descriptive results collected on the restored and control plots for the three faunal classifications, a. infauna, b. epifauna, and c. pelagic fauna

Source	Restored plots	Control plots
<b>a. Infauna</b>		
Locations	4	4
Total cores	71	66
Total organisms	1051	3254
Total taxa	57	82
Polychaetes	69%	59%
Capitellidae	24.2%	14.1%
Spionidae	26.4%	8.9%
Lumbrineridae	3.2%	10.4%
Bivalves	16%	14%
<b>b. Epifauna</b>		
Locations	4	4
Total transects	23	22
Total organisms	1001	564
Total taxa	10	11
Macroalgae	296	158
Cats eye snails	239	44
Cushion seastars	204	120
Eleven-arm seastar	190	8
Sea cucumbers	24	1
Colonial ascidians	1	218
<b>c. Pelagic fauna</b>		
Locations	2	2
Total videos	11	12
Total organisms	4987	6170
Total taxa	10	9
Spotty wrasse	3970	5266
Triplefin fish	782	13
Jack mackerel	123	295
Kahawai	36	519
Blue Cod	27	8
Snapper	6	32

The percentages in the infauna are percent of total fauna collected

Chi-squared;  $X^2_{(47,137)} = 71.11$ ,  $P = 0.01$ ), and crustaceans [4.6 times higher; Chi-squared;  $X^2_{(16,137)} = 41.49$ ,  $P < 0.001$ ]. All individual taxa identified recorded higher abundances on the control plots, except one, the bivalve *Theora lubrica* (81 recorded on the restored plots, 67 on controls). For further details of recorded taxa see Online Resource 2.

## Multivariate comparisons

Infauna assemblages were significantly affected by the addition of mussels (PERMANOVA;  $\text{PsF}_{1,136} = 16.351$ ;  $P = 0.001$ ), location (PERMANOVA;  $\text{PsF}_{3,136} = 9.839$ ;  $P = 0.001$ ), and sampling period (PERMANOVA;  $\text{PsF}_{1,136} = 5.304$ ;  $P = 0.001$ ) with significant interactions between location, the addition of mussels, and sampling period (PERMANOVA;  $\text{PsF}_{3,136} = 1.482$ ;  $P = 0.001$ ; for further details of PERMANOVA results see online resource 1). There was a clear separation between mussel and control plots in three of the four locations at both sampling periods (Fig. 2). There was also larger dissimilarity among restored plots (57.5%) than control plots (52.6%), indicating that the control plots are generally more similar to each other than the restored plots. A SIMPER analysis identified 15 taxa that were contributing to 70% of the dissimilarity between the mussel and control plots with the largest contribution from three polychaete families (Capitellidae 12.9%, Spionidae 9.5%, Lumbrineridae 9.5%). Polychaete families Capitellidae, Maldanidae, Syllidae, and Lumbrineridae were more abundant at control plots at both sampling periods, as were the bivalves *Corbula zealandica*, *Tawera spissa*, *Leptomysa retiaria*, and *Lincula hartvigiana* as identified by Pearson vector biplots (Fig. 2). The Bray–Curtis dissimilarity within the four locations was largest at Grant Bay (62.1%), followed by Te Mara (52.5%), Maori Bay (51.0%), and Skiddaw (47.5%). The dissimilarity was higher at 13-months (58.0%) than at 5-months (56%).

## Univariate comparisons

The total abundance of infaunal organisms was higher on the control plots than the restored plots at all locations (LME; d.f. = 6,  $F = 4.45$ ,  $P < 0.001$ ) and was higher at 13-months than 5-months only on the control plots (LME; interaction effect, d.f. = 1,  $F = 5.07$ ,  $P = 0.001$ ) (Fig. 3). The taxonomic richness was significantly higher on the control plots than the mussel plots (LME; d.f. = 4,  $F = 67.78$ ,  $P < 0.001$ ), and significantly differed between locations (LME; d.f. = 6,  $F = 7.53$ ,  $P < 0.001$ ), and sampling periods (LME; d.f. = 1,  $F = 20.18$ ,  $P < 0.001$ ). The Shannon–Wiener diversity index was higher on the control plots than the restored plots (LME; d.f. = 6,  $F = 6.85$ ,  $P < 0.001$ ) and was higher at 13-months than at 5-months only on the control plots (LME; d.f. = 1,  $F = 5.98$ ,  $P < 0.05$ ; Pairwise Wilcoxon test,  $P < 0.05$ ). Pielou’s evenness index was higher on the restored plots than the control plots (LME; d.f. = 4,  $F = 28.38$ ,  $P < 0.001$ ) and differed by location (LME; d.f. = 6,  $F = 16.25$ ,  $P < 0.001$ ), but not sampling period (LME; d.f. = 1,  $F = 2.46$ ,  $P > 0.05$ ; for further details of all LME results see Online Resource 1).

## Epifauna

Over the two sampling periods a total of 1001 individual epifaunal organisms from 10 taxa were sampled on the restored plots (23 total plots), while 564 organisms from 11 taxa were sampled from the control plots (22 total plots; Table 2). There were overall 13 taxa recorded with the most abundant being (in descending order): macroalgae (all non-encrusting brown, red, and green algae), cushion seastars (*Patriella regularis*—a common biofilm grazer), cat’s eye snails (*Lunella smaragda*—a common grazing marine gastropod), eleven-armed seastars (*C. muricata*—a shellfish predator), and colonial ascidians (a common filter feeder). Five taxa recorded higher abundance on the restored plots than on the

**Fig. 3** Differences on restored mussels (black) versus control plots (grey) for total abundance of the three classifications: **a** infauna, **b** epifauna, and **c** pelagic fauna, recorded over 5- and 13-months. Locations are in sediment gradient order of high coarse sand (right) to low coarse sand (left) and are abbreviated Grant Bay (GB), Maori Bay (MB), Skiddaw (SK), Te Mara (TM), means are reported ( $\pm$  SE)

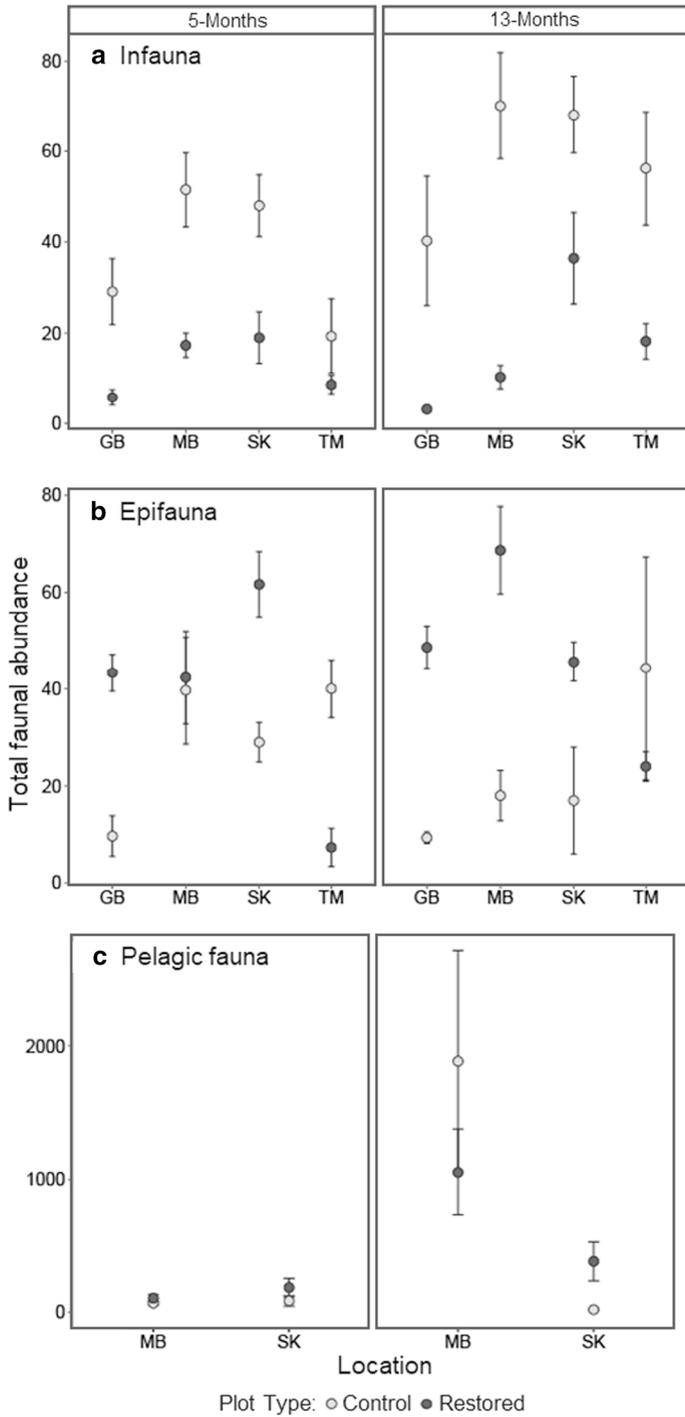
adjacent control plots: sea cucumbers (*Australostichopus mollis*, 23 times higher), eleven-armed seastars (22.7 times higher), cat's eye snails (5.2 times higher), macroalgae (1.8 times higher), and cushion seastars (1.6 times higher). Colonial ascidians were rarely found in the restored plots ( $n=1$ , TM) and were only detected in control plots at two locations ( $n=25$  at SK,  $n=193$  at TM). Eleven-armed seastars were rarely found on the control plots ( $n=8$ ) but were common throughout all restored plots with the highest abundance found at Grant Bay (total  $n=190$ , with  $n=159$  at GB). Horse mussels (*Atrina zelandica*) were only recorded on control plots ( $n=7$  at TM,  $n=1$  at SK). Macroalgae recorded similar numbers on the control and restored plots at the 5-month sampling (total control  $n=136$ , restored  $n=163$ ), but was rarely recorded in the control plots at 13-months (total control  $n=22$ , restored  $n=133$ ). Six taxa had five or less observations recorded overall (chiton, fan worms, limpets, sponges, sea urchins, whelks). For further details of recorded taxa see Online Resource 2.

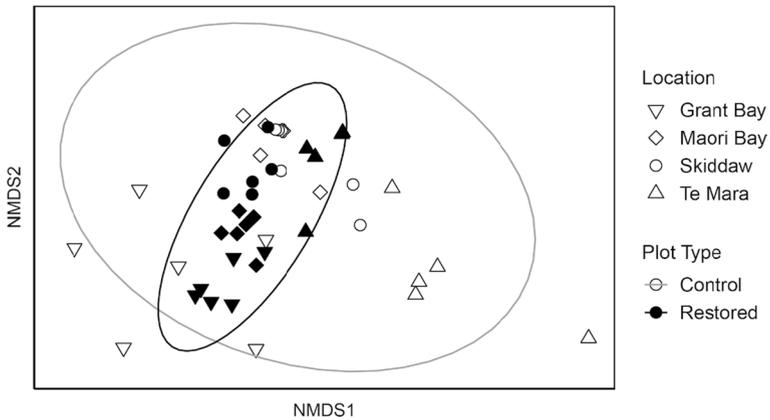
### Multivariate comparisons

Epifaunal assemblages were significantly affected by the addition of mussels (PERMANOVA;  $\text{PsF}_{1,44}=10.805$ ;  $P=0.001$ ), and location (PERMANOVA;  $\text{PsF}_{3,44}=13.776$ ;  $P=0.001$ ), but not by sampling period (PERMANOVA;  $\text{PsF}_{1,44}=1.975$ ;  $P>0.05$ ; for further details of PERMANOVA results see Online Resource 1). The assemblages of epifaunal organisms were more closely taxonomically related among the restored plots within each location than for their matching control plots, although the two treatments were not always clearly separated (Fig. 4). This was further shown by the Bray–Curtis dissimilarity estimates indicating a larger dissimilarity among control plots (56.1%) than restored plots (44.7%). The taxa that made the largest contribution to the dissimilarity within the treatments were also the most abundant groups: macroalgae (26.3%), cat's eye snails (20.2%), eleven-armed seastars (17.7%), and cushion stars (16.3%). The Bray–Curtis dissimilarity among the locations was largest at Te Mara (54.3%), followed by Grant Bay (41.9%), Maori Bay (40.4%), and Skiddaw (32.7%).

### Univariate comparisons

The total abundance of epifaunal organisms was higher on the restored plots than the control plots at three of the four locations (GB, MB, SK; LME; interaction effect, d.f.=3,  $F=10.76$ ,  $P<0.001$ ; Pairwise Wilcoxon test,  $P<0.05$ ), while the taxonomic richness was higher on the restored plots at two locations (GB, MB; LME; interaction effect, d.f.=3,  $F=3.11$ ,  $P<0.05$ ; Pairwise Wilcoxon test,  $P<0.05$ ). Both abundance and richness were not impacted by sampling period (LME; abundance, d.f.=1,  $F=0.02$ ,  $P>0.05$ ; richness, d.f.=1,  $F=0.95$ ,  $P>0.05$ ; Fig. 3). At Te Mara, the restored plots had a lower abundance than the other three locations (LME; interaction effect, d.f.=3,  $F=10.76$ ,  $P<0.001$ ; Pairwise Wilcoxon test,  $P<0.05$ ). The Shannon–Wiener diversity was higher on the restored plots at two of the four locations (MB, TM; interaction effect, LME; d.f.=1,  $F=9.39$ ,  $P<0.05$ ; Pairwise Wilcoxon test,  $P<0.01$ ), but Te Mara had significantly lower diversity





**Fig. 4** Non-metric multi-dimensional scaling (nMDS) for differences among epifauna community composition within control (open shapes) and restored plots (closed shapes) at the four locations (stress=0.14). Ellipses indicate 95% confidence interval

than Maori Bay on the restored plots (LME; interaction, d.f.=3,  $F=5.86$ ,  $P<0.01$ ; Pairwise Wilcoxon test,  $P<<0.05$ ). Diversity was not impacted by sampling period (LME; d.f.=1,  $F=1.08$ ,  $P>0.05$ ). Pielou's evenness index for epifauna was higher on the restored plots at Te Mara only (LME; interaction, d.f.=3,  $F=11.34$ ,  $p<0.001$ , Pairwise Wilcoxon test;  $P<0.05$ ), as the control plots at Te Mara lacked evenness due to the large number of colonial ascidians. For further details of all LME results see Online Resource 1.

## Pelagic fauna

Over the two sampling periods a total of 4987 individual pelagic fauna from 10 different taxa were identified on the restored plots from 11 cameras, while the control plots had 6170 individuals comprising of 9 taxa using 12 cameras (Table 2). Spotty wrasse (*Notolabrus celidotus*) is one of the most common coastal fish found at shallow depths in New Zealand and were the most observed species on both the mussel and control plots ( $n=9236$ , 83% of the total observations). Triplefin fish (Family Tripterygiidae, 7% of total), a small demersal blenny-like fish typically associated with rocky reefs, kahawai (*Arripis trutta*, 5% of total), a recreationally important pelagic fish often found in schools, and jack mackerel (Genus *Trachurus*, 4% of total), a midwater commercially important scombrid that is commonly found in schools, were the next most frequently observed fauna, with the remaining 1% composed of all the other taxa observed. Triplefin fish were observed 65.6 times more on the restored plots versus the control plots (total control  $n=13$ , restored  $n=782$ ), while blue cod (*Parapercis colias*), a commercially important demersal sandperch, were only recorded at Maori Bay where they were observed 3.7 times more often on the restored plots (total control  $n=8$ , restored  $n=27$ ). Spotty wrasse, kahawai, and jack mackerel were observed more times on the control plots (spotty wrasse  $n=5266$ , kahawai  $n=519$ , jack mackerel=295) versus the restored plots (spotty wrasse  $n=3970$ , kahawai  $n=36$ , jack mackerel=123). Snapper (*Chrysophrys auratus*), a commercially important demersal sparid, were recorded at 13-months (austral summer) but primarily on the control plots ( $n=32$  control,  $n=6$  mussel). New Zealand eagle rays (*Myliobatis tenuicaudatus*) and short-tailed rays (*Dasyatis brevicaudata*) were recorded in low overall abundances with

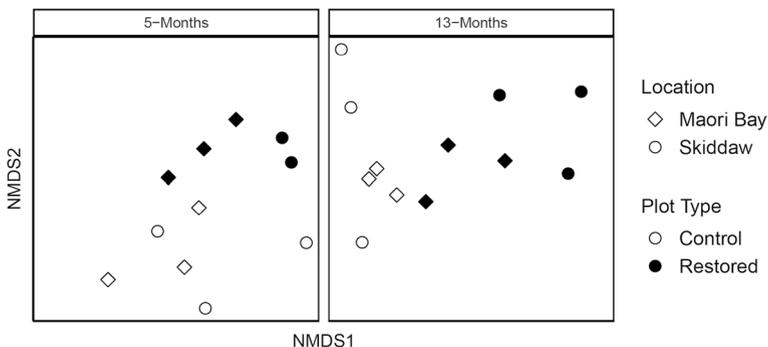
higher observations in the control plots than the restored (eagle ray, total control  $n=13$ , restored  $n=3$  mussel; short-tailed ray, total control  $n=11$ , restored  $n=2$  restored). For further details of recorded taxa see Online Resource 2.

### Multivariate comparisons

Pelagic fauna assemblages were significantly affected by the addition of mussels (PERMANOVA;  $\text{PsF}_{1,22}=7.963$ ;  $P=0.001$ ), location (PERMANOVA;  $\text{PsF}_{1,22}=5.1978$ ;  $P=0.005$ ), and sampling period (PERMANOVA;  $\text{PsF}_{1,22}=11.705$ ;  $P=0.001$ ), with significant interactions between location and sampling period (PERMANOVA;  $\text{PsF}_{1,22}=6.7553$ ;  $P=0.002$ ) and location and the addition of mussels (PERMANOVA;  $\text{PsF}_{1,22}=3.3349$ ;  $P=0.02$ ; for further details of PERMANOVA results see Online Resource 1). The pelagic assemblages are more closely related among the restored plots within each location than the control plots (~20 m away), where at each sampling period the two treatments were clearly separated according to the nMDS ordination model (Fig. 5). This was consistent with the larger dissimilarity among control plots (49.1%) than restored plots (41.9%) as shown by the Bray–Curtis dissimilarity analyses. A SIMPER analysis showed that the groups that made the largest contribution to the dissimilarity within the treatments were also the most abundant: spotty wrasse and triplefin fish (88.0%). The Bray–Curtis dissimilarity within the locations was similar at Maori Bay (48.6%), and Skiddaw (48.4%). Furthermore, the dissimilarity was higher at 13-months (46.8%) than at 5-months (38.6%), with spotty wrasse mostly responsible for the dissimilarity between sampling periods (SIMPER 73.0%).

### Univariate comparisons

The total abundance of pelagic organisms was higher at Maori Bay than at Skiddaw at 13-months (LME; interaction effect,  $\text{d.f.}=1$ ,  $F=8.04$ ,  $P<0.05$ ), and was higher at 13-months than at 5-months at Maori Bay (LME; interaction effect,  $\text{d.f.}=1$ ,  $F=8.04$ ,  $P<0.05$ ). However, the abundance of pelagic organisms was higher on the restored plots than on the control plots only at Skiddaw (Pairwise Wilcoxon test;  $P<0.01$ ; Fig. 3). Shannon–Weiner diversity index did not differ by location, the addition of mussels, or by



**Fig. 5** Non-metric multi-dimensional scaling (nMDS) for differences among pelagic fauna assemblages in the restored (closed shapes) and control plots (open shapes) at two study locations over the two sampling periods (5-months, 13-months; stress = 0.17)

sampling period (LME; location,  $d.f. = 1$ ,  $F = 0.19$ ,  $P > 0.05$ ; addition of mussels,  $d.f. = 1$ ,  $F = 0.005$ ,  $P > 0.05$ ; sampling period,  $d.f. = 1$ ,  $F = 3.65$ ,  $P > 0.05$ , Fig. 3). The taxonomic richness of the pelagic fauna was higher at 13-months than at 5-months only at Maori Bay (LME; interaction effect;  $d.f. = 1$ ,  $F = 15.07$ ,  $P < 0.01$ ), and at 13-months at Maori Bay the control plots had higher taxonomic richness than the restored plots (LME; interaction effect;  $d.f. = 1$ ,  $F = 6.16$ ,  $P < 0.05$ ). Pielou's evenness index was higher at Skiddaw than Maori Bay, but only at 13-months (LME; interaction effect;  $d.f. = 1$ ,  $F = 10.26$ ,  $P = 0.01$ ), while the addition of mussels had no impact (LME;  $d.f. = 1$ ,  $F = 0.16$ ,  $P > 0.05$ ; for further details of all LME results see Online Resource 1).

## Discussion

The decline in the extent of habitat-forming species, such as reef-forming shellfish, has contributed to a dramatic decline in biodiversity in coastal and marine environments throughout the world (zu Ermgassen et al. 2020). Restoration of these habitat-forming species can help to reinstate the ecosystem services they provide, including increasing the biodiversity and corresponding resilience of coastal ecosystems to future anthropogenic stressors (McLeod et al. 2019b; zu Ermgassen et al. 2020). Pilot-scale restoration has the potential to provide valuable information regarding the effect of shellfish restoration on biodiversity to guide subsequent decisions for larger scale restoration efforts. In this restoration trial, the addition of mussels to the seafloor overall resulted in a general reduction of infaunal species abundance and biodiversity, with a concomitant increase in epifaunal and pelagic species abundances, specifically from those species that benefit from benthic habitat complexity and an increase in food availability.

The markedly lower diversity and abundance of infaunal organisms associated with restoring mussels observed in this current study appear to be a result of differences in organic enrichment and sediment grain size. Increases in organic content and fine benthic sediments have both been shown to alter infaunal biodiversity for a range of habitats (Gray 2002; Kemp et al. 2005; Sciberras et al. 2017; Drylie et al. 2020), although some studies of remnant wild shellfish reefs have found a high abundance and diversity of infauna regardless of the underlying sediment (Commuto et al. 2008; van der Ouderaa et al. 2021). The underlying soft sediment at the four experimental locations varied in the quantity of the fine sediment (i.e., clay and silt). Observed changes in organic enrichment and grain size occurred within the first 5-months but there was no difference between 5- and 13-months, which indicates that these changes in the sediment occurred within the first 5-months after installing the mussels and did not continue to accumulate from 5 to 13-months. Mussels produce faeces and pseudo-faeces causing organic enrichment of the surrounding sediment (Commuto et al. 2008; Norling and Kautsky 2008; Donadi et al. 2014) and remove suspended fine sediment as they filter water (Christianen et al. 2017). The extent of organic enrichment of sediment in wild shellfish habitats has been shown to vary between different intertidal benthic environments (van der Ouderaa et al. 2021), and in this current study the greatest magnitude change was evident at Grant Bay, which may be due to the coarser composition of the sediment that characterised this site. The sediment organic content recorded in the four study locations was generally higher than measured for wild intertidal mussel habitats in the Netherlands (5.8% mussel, 0.9% control), however when compared to control sites the mussel habitats had a similar, higher amount of silt (1.3 times higher) and sediment organic content (6.4 times higher) as seen in our study (Christianen et al. 2017).

While the magnitude of the change in benthic sediment composition associated with the restoration of the mussel habitat varied by location, an overall increase in organic content and fine sediment was always apparent, the timing and extent of which were concordant with an observed general decline in the abundance and diversity of infauna at most locations.

Infaunal organisms respond to changes in sediment grain size and organic enrichment in a variety of circumstances. For example, high density longline aquaculture of mussels can greatly enrich the organic content of the sediment below the farm, typically resulting in a decrease in biodiversity, but an increased abundance in opportunistic deposit feeding organisms, such as members of the deposit feeding polychaete family Capitellidae (Keeley et al. 2009; Keeley 2013). Furthermore, organic enrichment of the sediment lowers the available oxygen and increases sulphide levels, which can create unfavourable conditions for some infauna, such as suspension feeders (Thrush et al. 2003; Drylie et al. 2020; Handley et al. 2020). Sensitive infauna respond quickly and dramatically to a small change in organic enrichment. For example, sediment in a New Zealand estuary was experimentally enriched from 2.1 to 3.7% resulting in an 80% decrease in the abundance of infauna after 70 days (Drylie et al. 2020). This sensitivity in infauna can result in changes in functional groups of infaunal organisms (Greenfield et al. 2016; Drylie et al. 2020) and was demonstrated by polychaetes in this study by a ten-fold higher abundance of free-living scavenger polychaete family Lumbrineridae in the control plots. Whereas suspension and deposit feeding polychaetes of the family Spionidae appeared to be less sensitive, decreasing one-fold under restored enrichment. Deposit feeding capitellids contributed to the highest difference between restored and control plots, being in almost a two-fold higher abundance on the control plots. The overall lower abundance, diversity, and deposit feeding infauna in restored mussel plots in this study is opposite to what has been previously recorded on wild shellfish reefs (Commuto et al. 2008; McLeod et al. 2013; van der Ouderaa et al. 2021). However, this study indicates a similar outcome for infauna as reported in these previous studies, that mussels facilitate certain infauna and inhibit others. This inhibition appears to be within the first 5-months for sensitive infauna, while the facilitation that leads to a high abundance of infauna seen in wild reefs may take more than 13-months on restored mussel habitats.

For epifauna, the addition of mussels to the seabed caused an increase in taxonomic richness and abundance across nearly every location within the first 5-months, likely as a result of the increase in habitat complexity, especially the provision of hard surfaces (i.e., mussel shells) provided by the restored mussels themselves. This habitat complexity is associated with elevated abundance and diversity of epibenthic organisms (e.g., Grabowski et al. 2005; McLeod et al. 2013) through the provision of habitat, food, and protection (Coen et al. 2007; Christianen et al. 2017). Despite differences in pre-existing epifauna among study locations, the installation of mussels resulted in the establishment of a similar assemblage of epifauna at all locations by 5-months, and thereafter. This was particularly evident for mobile epifauna, such as sea cucumbers, cat's eye snails, eleven-armed and cushion seastars, that were all found in higher abundances in the mussel plots, indicating a preference for this restored habitat and the increased food availability it provides. For example, sea cucumbers were likely attracted to mussel plots by increases in organic matter (Slater et al. 2011; Zamora and Jeffs 2011; Sea et al. 2022) and eleven-arm seastars are known mussel predators (Wilcox and Jeffs 2019). These organisms appeared to have migrated into the mussel habitats judging from their large observed sizes. Observed differences among study locations in mobile epifaunal diversity could be the result of differences in nearby source populations. For example, the higher concentration of eleven-arm seastars

at Grant Bay may be due its proximity to a marine farm, as higher concentrations of these seastars occur under farms (Inglis and Gust 2003). To aid in the restored mussel survival the seastars were collected and relocated throughout the sampling period, which may have influenced the overall epifaunal numbers. However, the observed continued migration of seastar predators into these small-scale trial plots indicate that it is important to consider location selection for restoration because proximity of sources of mussel predators may impact restoration success (Wilcox and Jeffs 2019).

The Te Mara location had lower abundance, richness, diversity of epifaunal organisms and the lowest macroalgae abundance of all locations. This may be a result of the environmental conditions being unsuitable for macroalgae, given the low macroalgal abundance in general at Te Mara. Shellfish facilitate macroalgal growth due to the enrichment of the benthic environment and the availability of hard substrate to settle and attach (Kemp et al. 2005; Norling and Kautsky 2008). The establishment of macroalgae could be an important process because it has been shown to facilitate mussel recruitment through providing larval and early juvenile settlement surfaces (Buchanan and Babcock 1997; Alfaro et al. 2004). Macroalgae also increase biodiversity by providing habitat and food for other organisms and have been shown to decrease the impact of ocean acidification on marine bivalves (Young and Gobler 2018). In this study a two-fold increase in macroalgal cover was found on the restored plots, which was driven by a large difference in macroalgae abundance between the control and mussel plots by 13-months. This indicates that macroalgae may take longer to establish on restored mussel habitats than other epifauna groups or seasonal factors were more important. The absence of juvenile sessile organisms seen in this study suggests that the establishment of biodiversity through less mobile epifauna may take longer than 13-months.

The installation of mussels substantially increased the abundance of demersal pelagic fauna at the two sampled locations, most likely as a result of attraction to the structure and associated biomass generated by the restored reefs (Powers et al. 2003; Parsons et al. 2016). For example, blue cod and triplefin fish are both demersal fish species that were observed more frequently on the restored mussel plots, although blue cod were only observed at Maori Bay potentially due to limitations in the range of this species (Beentjes et al. 2012). Blue cod are an endemic commercially and recreationally important species in New Zealand's South Island that are reported to have a significantly depleted population in the study area (Beentjes et al. 2012) and choosing restoration locations within their species ranges is vital for creating habitats for this vulnerable species. Triplefin fish are known to inhabit shellfish aquaculture farms (Morrisey et al. 2006) and are attracted to locations with more structural complexity where they can find refuge and protection (Feary and Clements 2006). These small fish are important trophically as they contribute to the diets of many larger species, including New Zealand's commercially important snapper (Jones 2013). Therefore, triplefin fish contribute to further higher trophic level pelagic diversity, which is important for ecosystem restoration and long-term resilience. In this study triplefin fish were observed 66 times more frequently on the mussel habitats than on adjacent soft sediment. Similarly, higher numbers of small fishes have been recorded in two studies in the North Island of New Zealand, one on remanent mussel reefs (14× higher; McLeod et al. 2013) and one on 6-year-old restored mussel habitats (16× higher; Sea et al. 2022). Blue cod diet consists of crustaceans, molluscs and polychaetes (Jiang and Carbines 2002) and triplefin fish diets consist of small mobile benthic invertebrates like crustaceans and molluscs (Feary et al. 2009), with both known to be opportunistic feeders based on their habitats (Jiang and Carbines 2002; Feary et al. 2009). Shellfish reefs have been shown to alter predator- prey interactions (Donadi et al. 2015) and be important feeding grounds for

fish (Lenihan et al. 2001), so the increase of these species on the restored plots may have reduced the resident invertebrate communities. Snapper and eagle rays are known to prey on mussels (Alder et al. 2021), however there was low numbers of snapper recorded overall in this study, which was unlikely to largely impact mussel survival.

Shellfish reefs are also known to serve as nurseries for fish (Knoche et al. 2020; zu Ermgassen et al. 2020), although only adult fish were recorded in this study. The lack of conspicuous fish recruitment in mussel plots may be the result of the small size of the restored plots, the cryptic nature of juvenile fish, or because the ecosystem is not established yet. The differences in pelagic community changes seen between 5-months and 13-months most likely reflect seasonal variation, where fish migrate to Pelorus Sound during the warmer summer temperatures (i.e., 13-month sampling). Not all pelagic fauna respond to restored shellfish habitats in the same way, and this was seen in this study particularly from non-demersal fishes such as spotty wrasse, jack mackerel, and kahawai that were observed in higher abundances in the control plots. Choosing restoration locations within species ranges that will benefit from an increase in benthic habitat complexity may therefore increase the pelagic diversity associated with restored shellfish habitats.

Trial pilot-scale restoration plots are recommended by shellfish restoration global guidelines to assess habitat suitability and understand which restoration techniques are needed before scaling up efforts (Fitzsimons et al. 2020). The results of this study indicate that pilot-scale restoration is also effective in determining biodiversity outcomes that can provide valuable information to guide subsequent decisions for larger scale restoration efforts. However, with the nature of pilot studies, this study was short-term (13-months) and had small sized plots, so the results do not show biodiversity changes over multiple seasons, which may be why there was no identified larval recruitment into the mussel plots. In oyster restoration it has been shown that after 6 years a restored oyster reef matches natural reefs biomass and ecosystem function (Smith et al. 2022), indicating that this an early look into restored mussel habitats and may not be representative of the biodiversity that occurs on restored mussel habitats long-term. Additionally, with the size of the mussel plots, the results are representative of an area of a restored mussel habitat but may not necessarily be representative of a larger scale restored mussel bed. This study does, however, provide the first understanding of what occurs on small-scale restored mussel habitats within the first-year post-restoration at multiple faunal classifications and the results can be used to improve location selection to enhance biodiversity on large scale restoration efforts.

The loss of ecosystem engineers, such as reef building shellfish, is generally recognized as a major threat to marine biodiversity, yet the lack of understanding of the recovery of biodiversity on restored shellfish reefs could limit restoration initiatives. Understanding marine biodiversity outcomes associated with restoring mussel habitats is important for restoring lost ecosystem services, including juvenile fish nurseries and habitat generation, along with long-term ecosystem resilience. From a management perspective, the results provided in this study highlight location-specific factors that should be considered to maximise biodiversity when restoring mussel habitats. Important factors include sediment composition and environmental conditions for macroalgae growth. Potential factors that were observed in this study that could also be considered when choosing locations to restore mussel habitats are nearby sources of species including predators, and ranges of important demersal fish. Small-scale pilot studies, like this one, can be used to inform management and improve overall biodiversity outcomes for future larger scale shellfish restoration. This deeper understanding of the biodiversity response in restored shellfish habitats is invaluable for justifying shellfish restoration initiatives and advancing efforts to restore vital foundation species and the habitats they create.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10531-022-02462-1>.

**Acknowledgements** We are grateful to Louis Olsen, Megan Carter, and Jon Stead for their contribution to the field work. Anna Bradley, Andrew Miller and volunteers; Chandini Skumar, Tammy Ranson, Pauline Raimbault, Matthew Williamson, Lida Flores, Yvonne Davis, and Wayne Downing for their help with laboratory work and video analysis. This study was carried out as part of a project, funded by the New Zealand Marine Farming Association, The Nature Conservancy, and the Ministry for Primary Industries, with support from Te Tau Ihu Fisheries Forum.

**Author contributions** EB, JH, AJ, and SH all contributed to the study design. EB, SH, TT, and RH contributed to the data collection. All authors contributed to the manuscript and have read and approved the final manuscript.

**Funding** Open Access funding enabled and organized by CAUL and its Member Institutions. This work was supported by the New Zealand Ministry for Primary Industries through the Sustainable Farming Fund project #405860.

**Data availability** The datasets are available from the corresponding author on request.

## Declarations

**Conflict of interest** The authors have no relevant financial or non-financial interests to disclose.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Alder A, Jeffs A, Hillman JR (2021) Considering the use of subadult and juvenile mussels for mussel reef restoration. *Restor Ecol* 29:1–10. <https://doi.org/10.1111/rec.13322>
- Alfaro AC, Jeffs AG, Creese RG (2004) Bottom-drifting algal/mussel spat associations along a sandy coastal region in northern New Zealand. *Aquaculture* 241:269–290. <https://doi.org/10.1016/j.aquaculture.2004.07.029>
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46. <https://doi.org/10.1046/j.1442-9993.2001.01070.x>
- Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw*. <https://doi.org/10.18637/jss.v067.i01>
- Beck MW, Brumbaugh RD, Airoidi L, et al (2009) Shellfish reefs at risk: a global analysis of problems and solutions. Arlington, VA. <https://www.conservationgateway.org/ConservationPractices/Marine/Documents/ShellfishReefsAtRisk-06.18.09-Pages.pdf>
- Beck MW, Brumbaugh RD, Airoidi L et al (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience* 61:107–116. <https://doi.org/10.1525/bio.2011.61.2.5>
- Beentjes MP, Page M, Sutton C, Olsen L (2012) Relative abundance, size and age structure, and stock status of blue cod from the 2010 survey in marlborough sounds, and review of historical surveys New Zealand Fisheries Assessment Report 2012/43. Ministry for Primary Industries, Wellington, NZ
- Buchanan S, Babcock R (1997) Primary and secondary settlement by the greenshell mussel *Perna canaliculus*. *J Shellfish Res* 16:71–76

- Christianen MJA, van der Heide T, Holthuijsen SJ et al (2017) Biodiversity and food web indicators of community recovery in intertidal shellfish reefs. *Biol Conserv* 213:317–324. <https://doi.org/10.1016/j.biocon.2016.09.028>
- Clarke K, Green R (1988) Statistical design and analysis for a “biological effects” study. *Mar Ecol Prog Ser* 46:213–226. <https://doi.org/10.3354/meps046213>
- Clarke K, Gorley R (2015) PRIMER v7, user manual/Tutorial. Primer-E, Plymouth
- Coen LD, Brumbaugh RD, Bushek D et al (2007) Ecosystem services related to oyster restoration. *Mar Ecol Prog Ser* 341:303–307. <https://doi.org/10.3354/meps341303>
- Commuto JA, Celano EA, Celico HJ et al (2005) Mussels matter: postlarval dispersal dynamics altered by a spatially complex ecosystem engineer. *J Exp Mar Biol Ecol* 316:133–147. <https://doi.org/10.1016/j.jembe.2004.10.010>
- Commuto JA, Como S, Grupe BM, Dow WE (2008) Species diversity in the soft-bottom intertidal zone: biogenic structure, sediment, and macrofauna across mussel bed spatial scales. *J Exp Mar Biol Ecol* 366:70–81. <https://doi.org/10.1016/j.jembe.2008.07.010>
- Donadi S, van der Zee EM, van der Heide T et al (2014) The bivalve loop: intra-specific facilitation in burrowing cockles through habitat modification. *J Exp Mar Biol Ecol* 461:44–52. <https://doi.org/10.1016/j.jembe.2014.07.019>
- Donadi S, Eriksson BK, Lettmann KA et al (2015) The body-size structure of macrobenthos changes predictably along gradients of hydrodynamic stress and organic enrichment. *Mar Biol* 162:675–685. <https://doi.org/10.1007/s00227-015-2614-z>
- Drylie TP, Lohrer AM, Needham HR, Pilditch CA (2020) Taxonomic and functional response of estuarine benthic communities to experimental organic enrichment: consequences for ecosystem function. *J Exp Mar Biol Ecol* 532:151455. <https://doi.org/10.1016/j.jembe.2020.151455>
- FAO (2021) The state of food and agriculture 2021. Making agrifood systems more resilient to shocks and stresses. FAO, Rome
- Feary DA, Clements KD (2006) Habitat use by triplefin species (Tripterygiidae) on rocky reefs in New Zealand. *J Fish Biol* 69:1031–1046. <https://doi.org/10.1111/j.1095-8649.2006.01178.x>
- Feary DA, Wellenreuther M, Clements KD (2009) Trophic ecology of New Zealand triplefin fishes (Family Tripterygiidae). *Mar Biol* 156:1703–1714. <https://doi.org/10.1007/s00227-009-1205-2>
- Fitzsimons JA, Branigan S, Gillies CL et al (2020) Restoring shellfish reefs: global guidelines for practitioners and scientists. *Conserv Sci Pract* 2:e198. <https://doi.org/10.1111/csp2.198>
- Flaws DE (1975) Aspects of the biology of the mussel in the Cook Strait area. Ph.D. Thesis, Victoria University
- Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. Sage, Thousand Oaks. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Gillies CL, McLeod IM, Alleyway HK et al (2018) Australian shellfish ecosystems: past distribution, current status and future direction. *PLoS ONE* 13:e0190914. <https://doi.org/10.1371/journal.pone.0190914>
- Grabowski JH, Hughes AR, Kimbro DL, Dolan MA (2005) How habitat setting influences restored oyster reef communities. *Ecology* 86:1926–1935. <https://doi.org/10.1890/04-0690>
- Gray JS (2002) Species richness of marine soft sediments. *Mar Ecol Prog Ser* 244:285–297. <https://doi.org/10.3354/meps244285>
- Greenfield BL, Kraan C, Pilditch CA, Thrush SF (2016) Mapping functional groups can provide insight into ecosystem functioning and potential resilience of intertidal sandflats. *Mar Ecol Prog Ser* 548:1–10. <https://doi.org/10.3354/meps11692>
- Handley S (2015) The history of benthic change in Pelorus Sound (Te Hoiere), Marlborough. In: National Institute of Water and Atmospheric Research Client Report Prepared for Marlborough District Council, NEL2015-001, pp. 47. <https://www.marlborough.govt.nz/environment/coastal/historical-ecosystem-change>
- Handley SJ, Morrisey D, Depree C et al (2020) Relative macrofaunal biomass reduced under an enriched salmon farm, Pelorus Sound, Aotearoa-New Zealand. *Mar Pollut Bull* 157:111303. <https://doi.org/10.1016/j.marpolbul.2020.111303>
- Heip C, Engels P (1974) Comparing species diversity and evenness indices. *J Mar Biol Assoc U K* 54:559–563. <https://doi.org/10.1017/S0025315400022748>
- Inglis GJ, Gust N (2003) Potential indirect effects of shellfish culture on the reproductive success of benthic predators. *J Appl Ecol* 40:1077–1089. <https://doi.org/10.1111/j.1365-2664.2003.00860.x>
- Jeffs A, Holland R, Hooker S, Hayden B (1999) Overview and bibliography of research on the greenshell mussel, *Perna canaliculus*, from New Zealand waters. *J Shellfish Res* 18:347–360
- Jiang W, Carabines G (2002) Diet of blue cod, *Paraperca colias*, living on undisturbed biogenic reefs and on seabed modified by oyster dredging in Foveaux Strait, New Zealand. *Aquat Conserv Mar Freshw Ecosyst* 12:257–272. <https://doi.org/10.1002/aqc.495>

- Jones GP (2013) Ecology of rocky reef fish of northeastern New Zealand: 50 years on. *New Zeal J Mar Freshw Res* 47:334–359. <https://doi.org/10.1080/00288330.2013.812569>
- Keeley N (2013) Literature review of ecological effects of aquaculture, benthic effects. New Zealand Ministry of Primary Industries, p 33. <https://www.mpi.govt.nz/dmsdocument/3751-literature-review-of-ecological-effects-of-aquaculture-chapter-3-benthic-effects>
- Keeley N, Forrest B, Hopkins G, et al (2009) Sustainable aquaculture in New Zealand: review of ecological effects of farming shellfish and other non-fish species. In: Cawthron client report prepared for Ministry of Fisheries, report no. 1476, p 150
- Kemp WM, Boynton WR, Adolf JE et al (2005) Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Mar Ecol Prog Ser* 303:1–29. <https://doi.org/10.3354/meps303001>
- Knoche S, Ihde TF, Samonte G, et al (2020) Estimating ecological benefits and socio-economic impacts from oyster reef restoration in the Choptank river complex, Chesapeake Bay. NOAA Tech. Memo. NMFS-OHC-6, p 68
- Kruskal JB, Wish M (1978) Multidimensional scaling. Sage, Beverly Hills, CA, USA
- Lenihan HS, Peterson CH, Byers JE et al (2001) Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. *Ecol Appl* 11:764. <https://doi.org/10.2307/3061115>
- Lotze HK, Lenihan HS, Bourque BJ et al (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809. <https://doi.org/10.1126/science.1128035>
- McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290–297. [https://doi.org/10.1890/0012-9658\(2001\)082\[0290:FMMTCD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2)
- McLeod IM, Parsons DM, Morrison MA et al (2012) Factors affecting the recovery of soft-sediment mussel reefs in the firth of Thames, New Zealand. *Mar Freshw Res* 63:78–83. <https://doi.org/10.1071/MF11083>
- McLeod I, Parsons D, Morrison M et al (2013) Mussel reefs on soft sediments: a severely reduced but important habitat for macroinvertebrates and fishes in New Zealand. *New Zeal J Mar Freshw Res* 48:48–59. <https://doi.org/10.1080/00288330.2013.834831>
- McLeod IM, Bostrom-Einarsson L, Creighton C et al (2019a) Habitat value of Sydney rock oyster (*Saccostrea glomerata*) reefs on soft sediments. *Mar Freshw Res* 71:771–781. <https://doi.org/10.1071/MF18197>
- McLeod IM, zu Ermgassen PSE, Gillies CL, et al (2019b) Can bivalve habitat restoration improve degraded estuaries? Coasts and estuaries: the future. Elsevier, Amsterdam, pp 427–442
- Morrisey DJ, Cole RG, Davey NK et al (2006) Abundance and diversity of fish on mussel farms in New Zealand. *Aquaculture* 252:277–288. <https://doi.org/10.1016/j.aquaculture.2005.06.047>
- Newell R (2004) Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *J Shellfish Res* 23:51–61
- Norling P, Kautsky N (2008) Patches of the mussel *Mytilus* sp. are islands of high biodiversity in subtidal sediment habitats in the Baltic Sea. *Aquat Biol* 4:75–87. <https://doi.org/10.3354/ab00096>
- Oksanen J, Blanchet GF, Friendly M et al (2020) vegan: community ecology package. <https://cran.r-project.org, https://github.com/vegandevs/vegan>
- Parker JG (1983) A comparison of methods used for the measurement of organic matter in marine sediment. *Chem Ecol* 1:201–209. <https://doi.org/10.1080/02757548308070802>
- Parsons DM, Buckthought D, Middleton C, MacKay G (2016) Relative abundance of snapper (*Chrysophrys auratus*) across habitats within an estuarine system. *New Zeal J Mar Freshw Res* 50:358–370. <https://doi.org/10.1080/00288330.2016.1146310>
- Parsons DM, Buckthought D, Edhouse S, Lohrer AM (2020) The paradox of the Hauraki Gulf snapper population: testing the nursery habitat concept. *Mar Ecol* 41:1–11. <https://doi.org/10.1111/maec.12582>
- Paul-Burke K, Burke J (2013) Monitoring assessment of kūtai (*Perna canaliculus*) green-lipped mussel and pātangaroa (*Coscinasterias muricata*) seastar populations in the western side of Ōhiwa Harbour 2013: technical report. Whakatāne, New Zealand: Te Rūnanga o Ngāti Awa
- Paul LJ (2012) A history of the Firth of Thames dredge fishery for mussels: use and abuse of a coastal resource. New Zealand Aquatic Environment and Biodiversity rep no 94, p 27. <http://www.maf.govt.nz/news-resources/publications.aspx>
- Pielou EC (1966) The measurement of diversity in different types of biological collections. *J Theor Biol* 13:131–144. [https://doi.org/10.1016/0022-5193\(66\)90013-0](https://doi.org/10.1016/0022-5193(66)90013-0)
- Powers SP, Grabowski JH, Peterson CH, Lindberg WJ (2003) Estimating enhancement of fish production by offshore artificial reefs: uncertainty exhibited by divergent scenarios. *Mar Ecol Prog Ser* 264:265–277. <https://doi.org/10.3354/meps264265>
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

- Ray NE, Fulweiler RW (2021) Meta-analysis of oyster impacts on coastal biogeochemistry. *Nat Sustain* 4:261–269. <https://doi.org/10.1038/s41893-020-00644-9>
- Ray NE, Hancock B, Brush MJ et al (2021) A review of how we assess denitrification in oyster habitats and proposed guidelines for future studies. *Limnol Oceanogr Methods* 19:714–731. <https://doi.org/10.1002/lom3.10456>
- Schotanus J, Capelle JJ, Parea E et al (2020) Restoring mussel beds in highly dynamic environments by lowering environmental stressors. *Restor Ecol* 28:1124–1134. <https://doi.org/10.1111/rec.13168>
- Sciberras M, Tait K, Brochain G et al (2017) Mediation of nitrogen by post-disturbance shelf communities experiencing organic matter enrichment. *Biogeochemistry* 135:135–153. <https://doi.org/10.1007/s10533-017-0370-5>
- Sea MA, Hillman JR, Thrush SF (2022) Enhancing multiple scales of seafloor biodiversity with mussel restoration. *Sci Rep* 12:1–13. <https://doi.org/10.1038/s41598-022-09132-w>
- Slater MJ, Jeffs AG, Sewell MA (2011) Organically selective movement and deposit-feeding in juvenile sea cucumber, *Australostichopus mollis* determined in situ and in the laboratory. *J Exp Mar Biol Ecol* 409:315–323. <https://doi.org/10.1016/j.jembe.2011.09.010>
- Smith G (1985) The Queensland oyster fishery—an illustrated history. Queensland Department of Primary Industries, Brisbane
- Smith RS, Lusk B, Castorani MCN (2022) Restored oyster reefs match multiple functions of natural reefs within a decade. *Conserv Lett*. <https://doi.org/10.1111/conl.12883>
- Stead DH (1969) Fisheries technical report no. 62. Pelorus sound: mussel survey December 1969. Fisheries Division, Marine Department, Wellington
- Thrush SF, Hewitt JE, Norrko A et al (2003) Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. *Mar Ecol Prog Ser* 263:101–112. <https://doi.org/10.3354/meps263101>
- Toone TA, Hunter R, Benjamin ED et al (2021) Conserving shellfish reefs—a systematic review reveals the need to broaden research efforts. *Restor Ecol* 29:1–13. <https://doi.org/10.1111/rec.13375>
- Urlich SC, Handley SJ (2020) From ‘clean and green’ to ‘brown and down’: a synthesis of historical changes to biodiversity and marine ecosystems in the Marlborough Sounds, New Zealand. *Ocean Coast Manage* 198:105349. <https://doi.org/10.1016/j.ocecoaman.2020.105349>
- van der Ouderaa IBC, Claassen JR, van de Koppel J et al (2021) Bioengineering promotes habitat heterogeneity and biodiversity on mussel reefs. *J Exp Mar Biol Ecol* 540:151561. <https://doi.org/10.1016/j.jembe.2021.151561>
- Wallis B, Troost K, van den Ende D et al (2016) From artificial structures to self-sustaining oyster reefs. *J Sea Res* 108:1–9. <https://doi.org/10.1016/j.seares.2015.11.007>
- Wilcox M, Jeffs A (2019) Impacts of sea star predation on mussel bed restoration. *Restor Ecol* 27:189–197. <https://doi.org/10.1111/rec.12831>
- Wilcox M, Kelly S, Jeffs A (2018) Ecological restoration of mussel beds onto soft-sediment using transplanted adults. *Restor Ecol* 26:1–10. <https://doi.org/10.1111/rec.12607>
- Willis TJ, Babcock RC (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. *Mar Freshw Res* 51:755–763. <https://doi.org/10.1071/MF00010>
- Young CS, Gobler CJ (2018) The ability of macroalgae to mitigate the negative effects of ocean acidification on four species of North Atlantic bivalve. *Biogeosciences* 15:6167–6183. <https://doi.org/10.5194/bg-15-6167-2018>
- Zamora LN, Jeffs AG (2011) Feeding, selection, digestion and absorption of the organic matter from mussel waste by juveniles of the deposit-feeding sea cucumber, *Australostichopus mollis*. *Aquaculture* 317:223–228. <https://doi.org/10.1016/j.aquaculture.2011.04.011>
- zu Ermgassen P, Hancock B, DeAngelis B, Greene J, Schuster E, Spalding M, Brumbaugh R (2006) Setting objectives for oyster habitat restoration using ecosystem services: A manager’s guide. Arlington, The Nature Conservancy, p 76
- zu Ermgassen P, Grabowski JH, Gair JR, Powers SP (2016) Quantifying fish and mobile invertebrate production from a threatened nursery habitat. *J Appl Ecol* 53:596–606. <https://doi.org/10.1111/1365-2664.12576>
- zu Ermgassen PSE, Thurstan RH, Corrales J et al (2020) The benefits of bivalve reef restoration: a global synthesis of underrepresented species. *Aquat Conserv Mar Freshw Ecosyst* 30:2050–2065. <https://doi.org/10.1002/aqc.3410>