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Habitat factors affecting scallop spat survival and growth in Golden Bay and Tasman Bay

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PLAIN LANGUAGE SUMMARY

Scallops (*Pecten novaezelandiae*) play an important role in Aotearoa-New Zealand's coastal marine ecosystem, and they are highly valued as a taonga and fishery species. However, large declines in scallop numbers have occurred, and the main scallop fisheries are currently closed.

In some areas, seabed habitats appear degraded and no longer suitable for scallops, and poor habitat quality is thought to be the main barrier preventing scallop recovery.

In this study, we reviewed knowledge of scallop habitat preferences, and conducted a field experiment to investigate scallop survival and growth in relation to habitat characteristics. The field experiment was conducted in 2018 at a range of sites in Golden Bay and Tasman Bay, at the north of the South Island. Small juvenile scallops (spat) were marked and released at the sites in May, and the sites were surveyed by divers in June and December. Scallop spat survival was very low in muddy/simple habitats, and much higher in sandy/complex habitats.

The study suggests scallop population recovery may only be expected to occur in areas with suitable habitat.

EXECUTIVE SUMMARY

Williams, J.R.[1]; Tuck, I.D.; Hale, R.; Middleton, C.; Hughes, R.; Stead, J. (2024). Habitat factors affecting scallop spat survival and growth in Golden Bay and Tasman Bay.

***New Zealand Aquatic Environment and Biodiversity Report No. 342.* 67 p.**

Highly productive populations of scallops (*Pecten novaezelandiae*) that supported Aotearoa New Zealand's largest scallop fishery (SCA 7) at the north of the South Island underwent massive declines in the 2000s and have failed to recover despite scallop spat reseeding efforts and the cessation of fishing. A reduction in the quality and quantity of habitats that support scallops is thought to be the main barrier preventing population recovery, as habitats in key fishery areas appear degraded and no longer suitable for scallop spat settlement, survival, and growth. Determining the factors that are suppressing the survival and growth of scallops is required to inform the potential for restoration activities and scallop population recovery.

The overall aim of this project was to investigate environmental factors correlated with scallop survival and growth in SCA 7. Our research approach involved conducting a knowledge review and a field experiment. We reviewed the current knowledge of scallop habitat preferences for a range of related scallop species, and specifically for *P. novaezealandiae*. We investigated scallop-habitat associations by conducting a field study of scallops and their habitats across a range of sites with a variety of environmental conditions in Golden Bay and Tasman Bay at the north of New Zealand's South Island. Thousands of small juvenile scallops (spat) from collector bags were marked with calcein and released at the study sites in May 2018, and the sites were resurveyed by divers in June and December 2018. Data on scallop metrics (scallop spatial density, length frequency distribution, condition, disease) and habitat variables (sediment characteristics, seawater properties, benthic macrofaunal community, predator and habitat feature counts from video transects) were modelled using multivariate methods to identify the key habitat variables associated with scallop survival and growth.

The field study confirmed that although some sites provided suitably favourable habitats for scallop survival, the low numbers of scallops recovered from other sites in previously fished areas suggested those habitats were unsuitable. A variety of environmental and ecological habitat variables were associated with scallop survival. Scallop spat survival was low in muddy/simple habitats and high in sandy/complex habitats which also supported extant scallop populations. Growth was not significantly related to environmental parameters but the calculated growth estimates for some sites were based on small numbers of scallops recovered and may have been confounded by differential survival among sites.

Our findings are consistent with those of previous research: seabed sediment type and aspects of the benthic community (predators/scavengers) are important components of scallop habitat. Our study identified the habitat features that were strongly associated with scallop productivity metrics at sites in Golden Bay and Tasman Bay. These relationships could be used to predict which similar benthic environments outside the study area could support scallops and determine candidate sites for restoration and reseeding efforts. Our study established the patterns from which plausible hypotheses can be developed and tested in future research. Further investigation of scallop-habitat relationships in other scallop beds elsewhere in New Zealand was conducted during survey work in 2021, confirming that the patterns we found in our 2018 study also apply in other areas outside the relatively sheltered bays investigated here.

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[1] All authors affiliated with NIWA, New Zealand, at the time the work was undertaken.

1. INTRODUCTION

1.1 Overview

Scallop populations worldwide are renowned for high spatial and temporal variability in productivity (Orensanz et al. 2016). Despite the important ecosystem role of scallops and the high value of scallop fisheries globally, the factors affecting recruitment, growth, and mortality which collectively define productivity remain poorly understood. Research overseas demonstrates significant advances can be made through examining scallop habitat suitability (Brown et al. 2012, Mendo et al. 2014).

A suitable habitat for an organism can be defined as a place that has the environmental conditions (e.g., temperature, salinity, current flow, turbidity) and resources (e.g., food, oxygen, physical space, structure) that enable the organism to occur and persist there; habitat suitability is also affected by intra- and inter-specific interactions (e.g., competition, predation, disease) (Begon et al. 1990). In general there have been few experimental studies carried out that explore the effects of habitat (i.e., environmental and ecological) factors on scallop population dynamics, so little is known of the relative importance of specific factors (Brand 2016).

In Aotearoa New Zealand, highly productive populations of scallops (*Pecten novaezelandiae*) in Golden Bay and Tasman Bay that supported the nation's largest scallop fishery (SCA 7, at the north of the South Island) underwent massive declines in the 2000s and have failed to recover, despite juvenile scallop (spat) reseeding efforts and the cessation of fishing (Williams et al. 2014, Williams et al. 2021). A reduction in the quality and quantity of habitats that support scallops is thought to be the main barrier preventing population recovery, as habitats appear degraded and no longer suitable for scallop settlement, survival, and growth (Michael et al. 2015, Williams et al. 2019, Southern Scallop Working Group & Fisheries New Zealand 2020). Determining the factors that are suppressing the survival and growth of scallops is required to inform the potential for restoration activities and population recovery. Key to this is improving our understanding of what constitutes suitable habitat for scallops.

1.2 Objectives

The present study was conducted under Fisheries New Zealand project SCA2017-03: "Survey of environmental factors correlated with scallop survival and growth". The overall objective of the project was to examine scallop health indices across a range of environmental gradients in SCA 7. Specific research objectives were:

1) to map and characterise a gradient of environments within SCA 7 that potentially support scallops;
2) to sample and monitor a range of scallop indices across this gradient to determine factors suppressing settlement, growth, and survival of scallops in the previously productive parts of the fishery; and
3) to monitor the survival and growth of scallop spat across this gradient to determine suitable sites for scallop reseeding or other intervention.

1.3 Research approach

Our research approach addressed these objectives through conducting a knowledge review and a field experiment. We reviewed the current knowledge of scallop habitat preferences for a range of related scallop species found overseas, and specifically for *P. novaezealandiae* in New Zealand. We investigated scallop-habitat associations by conducting a field study of scallop biology in relation to habitat variables at a range of sites with a variety of environmental conditions in Golden Bay and Tasman Bay. We used prior information on scallop densities and historical and environmental characteristics within Objective 1 to determine study sites. Objectives 2 and 3 were addressed by monitoring scallop survival and growth across the study sites: thousands of juvenile scallops (spat) from

collector bags were marked with calcein and released at 10 sites in May 2018, and the sites were resurveyed by divers in June and December 2018. Data on scallop metrics (scallop spatial density, length frequency distribution, condition, and disease) and habitat variables (sediment characteristics, seawater properties, benthic macrofaunal community, predator and habitat feature counts from video transects) were modelled using multivariate methods to identify the key habitat variables associated with scallop survival and growth.

2. SCALLOP HABITAT KNOWLEDGE REVIEW

Comprehensive information on scallop biology, ecology, aquaculture, and fisheries was provided by Shumway & Parsons (2016), including the chapter by Brand (2016) which discusses scallop ecology (distributions and behaviour) in detail. The following review of scallop habitat knowledge primarily draws on relevant information from the international scallop studies referred to by Brand (2016) together with relevant information from New Zealand scallop studies.

2.1 International scallop studies

Scallops are marine bivalves of the Pectinidae family which has about 270 extant species recognised (Serb 2016), of which about 26 species occur in sufficient densities to support exploitable fisheries (Orensanz et al. 2016). The Pectinidae is a cosmopolitan family found in a wide range of habitats around the globe. Scallops are benthic for most of their life but have a feeding planktonic larval dispersal phase. Scallops are primarily free-living, although some species may attach themselves to solid objects, and many species are mobile both as juveniles and adults and are capable of moving or swimming short distances. Intrinsically, scallops can demonstrate habitat preferences for where they settle and reside during their life (Brand 2016). Scallops have spatially aggregated distributions in 'grounds' where individuals are found together in abundance (Brand 2016). The habitats in these grounds are suitable for scallops through the provision of species-specific environmental needs and are usually separated by areas that are environmentally unsuitable, leading to spatial patchiness in scallop density distributions.

Habitat, rather than larval supply, is probably the primary driving factor explaining recruitment variability (Caddy 1989, Hart et al. 2013) with habitat type a key factor identified in multiple post-settlement survival studies (Thouzeau et al. 1991, Howarth et al. 2011, Carey et al. 2013). Multiple habitat factors are known to influence the distribution of scallops, including temperature, water depth, substrate type, the availability of food (i.e., suspended detrital material and phytoplankton, or material resuspended by the scallops themselves), water currents, salinity, turbidity, and the occurrence of competitors and predators. These factors are often closely linked (e.g., temperature, food availability, and substrate type are often correlated with depth). For example, Mendo et al. (2014) examined the relationship between the distribution and abundance patterns of three species of scallop (*Pecten fumatus*, *Equichlamys bifrons*, and *Mimachlamys asperrima*) and associated habitat characteristics in D'Entrecasteaux Channel, Tasmania. The distribution of each species was related to sediment type and species-specific habitat structural components, with *P. fumatus* abundance strongly associated with fine sand sediments. Other important habitat characteristics were water depth and shell debris cover (scallop abundance increased with increasing shell debris on the surface of the seabed) and predation and macroalgae cover (scallop abundance decreased as macroalgae coverage and the abundance of starfish *Asterias amurensis* increased). As such, it is often difficult to assess the effect of any one habitat characteristic on the abundance and distribution of scallops (Brand 2016); however, a few general patterns have emerged.

Most scallops live in fully saline environments, and many do not survive prolonged exposure to low salinity (<31 ppm) conditions (e.g., *Argopecten gibbus* (Allen & Costello 1972); *Argopecten purpuratus* (Uribe et al. 2003); *Aequipecten opercularis* (Ursin 1956, Paul 1980); *Mizuhopecten yessoensis* (Ventilla 1982); *Adamussium colbecki* (Stockton 1984)). Vulnerability to salinity varies with species and life stage. Spat may be more (e.g., *Aequipecten opercularis* (Paul 1980); *Mimachlamys asperrima* (O'Connor & Heasman 1998)) or less (e.g., *Mizuhopecten yessoensis* (Yamamoto 1956); *Pecten*

maximus (Christophersen & Strand 2003); *Placopecten magellanicus* (Frenette & Parsons 2001)) tolerant of low salinity than juveniles and adults. Species adapted to living in estuarine environments may be more tolerant to salinity fluctuations (e.g., *A. irradians* (Mercaldo & Rhodes 1982)).

Temperature is a primary factor that limits the geographical range of most marine organisms, including scallops (Brand 2016). Temperature affects scallop physiology and growth: with increasing temperature, metabolic rate increases and growth efficiency (i.e., the quotient of production over assimilation) decreases across a wide range of pectinid populations and species (Heilmayer et al. 2004). Temperature tolerances are well understood for several scallop species (Brand 2016), or can be inferred from the annual range in temperatures observed across the species' geographic range.

Multiple habitat characteristics vary with water depth. For example, temperature variations control the depth distributions of *Argopecten gibbus* around Cape Canaveral, Florida, US (Miller & Richards 1980) and *Placopecten magellanicus* on the northwest Atlantic shelf from the Gulf of St Lawrence, Canada to North Carolina, USA (Bourne 1964), with temperature changes due to cold upwellings or increased sea surface temperatures and thermocline changes affecting population distributions and mortalities (Dickie & Medcof 1963, Miller et al. 1981). Food availability also varies with depth and can restrict scallop presence (e.g., *Aequipecten opercularis* in Denmark and the Faroe Islands (Ursin 1956)) and growth rates (e.g., *P. magellanicus* in Newfoundland (MacDonald & Thompson 1985a, b, 1986a, b, MacDonald et al. 1987) and Gulf of Maine (Schick et al. 1988)). As active suspension feeders, scallops require phytoplankton and other suspended material, some of which may be benthic microalgae that have become resuspended (Macdonald et al. 2006).

Commercial scallop species show a general preference for coarser sediments, ranging from fine sand to gravel substrates (Mason 1983, Young et al. 1989, Thouzeau et al. 1991, Stokesbury & Himmelman 1993, Dare et al. 1994). Although some species tolerate some silt or mud in their inhabiting substrate (e.g., *Amusium pleuronectes* (Young et al. 1989); *Argopecten gibbus* (Allen & Costello 1972); *Argopecten irradians* (Belding 1931, Gutsell 1931); *Pecten maximus* (Mason 1983); *Pecten fumatus* (Young & Martin 1989); *Placopecten magellanicus* (Bourne 1964)), faster growth rates are normally observed in areas with little mud (Brand 2016). Deposition of diatoms, an important food source for some scallop species, may be higher on coarser sandier sediments, (e.g., *P. magellanicus* (Pilditch et al. 1997)). The local hydrodynamic effects of coarse substrates have not only been linked to food deposition but also to reducing the current in the area around each scallop, which in turn improves scallop filtering efficiency (Bourgeois et al. 2006 and references therein). While coarse substrates are usually associated with strong benthic currents, some scallops prefer areas with slower currents (e.g., *Pecten maximus* (Dare et al. 1994); *Placopecten magellanicus* (Wildish et al. 1987, Wildish & Kristmanson 1988, Wildish & Saulnier 1992, 1993, Claereboudt et al. 1994a, Claereboudt et al. 1994b, Pilditch & Grant 1999); *Argopecten irradians* (Kirby-Smith 1972, Eckman et al. 1989); *Chlamys islandica* (Arsenault et al. 1997)). Coarse substrates also provide better attachment for small juvenile scallops (via byssus) that limit their dispersal (e.g., *P. magellanicus* (Caddy 1972, Hatcher et al. 1996)) and could help retain them in this habitat.

Structural complexity of the benthic habitat may also affect scallop health with features such as crevices (e.g., *C. islandica* (Arsenault et al. 1997)) providing shelter from currents and predators allowing increased growth rates. Erect algae and bryozoans may provide scallop spat with elevated silt-free settlement surfaces, above benthic boundary layer turbidity (Brand et al. 1980, Paul 1981, Dare & Bannister 1987, Harvey et al. 1994, Stokesbury & Himmelman 1995), and out of reach from some benthic predators. However, while settlement in seagrass beds may provide refuge from higher current flows (e.g., *A. irradians* (Eckman 1987)), it may also impede seawater flux at high plant densities and facilitate increased predation (e.g., *A. irradians* (Irlandi et al. 1999)). Conversely, while macroalgae may provide habitat complexity, it may also impede scallop suspension feeding: Valiela et al. (1992) related the long-term decline in *A. irradians* populations to the multiple effects of macroalgae reducing benthic oxygen levels, suppressing the efficiency of suspension feeding, and smothering the seagrass beds that provided sheltered habitat.

Also linked to benthic habitat complexity and sediment type, it is likely that turbidity is an important factor that limits the abundance and distribution of settled scallops (Brand 2016). While some species live in muddy environments that experience turbid conditions (e.g., inshore: *A. irradians* (Belding 1931); *Volachlamys tranquebaria* (Suresh et al. 2013); shallow subtidal: *Minnivola pyxidatus* (Morton 1996); and deep sea: *Chlamys septumradiata* (Allen 1953)) most scallops live in well-flushed coarser (sandy) sediment substrates and are not normally subject to high levels of bottom water turbidity (Brand 2016). Increased silt and particulate organic matter in the water column has a detrimental effect on the feeding and growth of some scallop species (e.g., *Chlamys islandica* (Vahl 1980, Wallace & Reinsnes 1985); *Mizuhopecten yessoensis* (Yamamoto 1956)). Increased organic matter input and associated decreased benthic oxygen concentrations can exacerbate the effects of seawater turbidity which can also cause spat mortality (e.g., *A. irradians* (Belding 1931); *M. yessoensis* (Yamamoto 1956, Yamamoto 1960)). Habitat disturbance resulting in higher turbidity (e.g., dredging and trawling) can have detrimental effects even on species adapted to high turbidity (e.g., *M. pyxidatus* (Morton 1996)).

Ecological interactions also structure scallop population distributions. Predation provides a top-down control on scallop numbers that is also influenced by habitat conditions, and by scallop and predator characteristics. Although spat and larger juvenile scallops are vulnerable to benthic predators that can limit the establishment and distribution of scallop populations (Brand 2016), few attempts have been made to determine predation rates on scallop spat in their natural environments (Powers & Kittinger 2002, Talman et al. 2004, Hart & Shank 2011). However, Shank et al. (2012) found that juvenile *P. magellanicus* predation, primarily by crabs (*Cancer* spp.), increased with scallop density. High densities of scallops can also increase predation rates as this tends to attract high densities of predators, which can then prey on vulnerable settlers (Caddy 1989, Hart & Shank 2011, Shank et al. 2012). As spat grow larger and their shells thicken, they become less vulnerable to some predators.

Often, predation is correlated with other environmental variables. For example, predation of *A. irradians* by whelks increased with current flow speed, whereas predation by blue crabs decreased; current flows affected chemosensory cues and scallop avoidance behaviours (Powers & Kittinger 2002). Dense populations of scallops, other bivalves, and other benthic filter feeders can lead to increased competition for suspended food particles which may limit settlement and growth of scallop populations in dense patches of other filter feeders (Woodin 1976, Lehane & Davenport 2002, Porri et al. 2008). However, these ecological controlling processes of predation and competition are not well understood and are difficult to study in isolation from other correlated environmental factors controlling both scallop and predator/competitor behaviour and physiology.

2.2 New Zealand scallop studies

There are 18 species of Pectinidae recorded from New Zealand, but only two, the New Zealand scallop *Pecten novaezealandiae* and the queen scallop *Zygochlamys delicatula*, occur at sufficient densities and sizes to be commercially exploited (Dredge et al. 2016, Fisheries New Zealand 2022). *Zygochlamys delicatula* is found around the east coast of the South Island south of Kaikōura, most commonly at depths below 130 m, whereas *P. novaezealandiae* inhabits coastal waters throughout New Zealand, including Stewart Island and the Chatham Islands, and inhabits waters down to 50 m with some individuals noted down to 90 m. *Pecten novaezealandiae* provides the larger fishery and plays an important role in the functioning of coastal marine ecosystems (Fisheries New Zealand 2022).

Pecten novaezelandiae is a functional hermaphrodite that reaches sexual maturity at a size of about 70 mm shell length (Williams & Babcock 2005). Mature adult scallops exhibit episodic broadcast spawning behaviour followed by gonad redevelopment, with the main spawning events occurring in spring and early summer (Williams & Babcock 2004). Fecundity increases exponentially with scallop size: Year 1 scallops contain about 500 000 eggs, whereas year 4 and 5 scallops can contain over 40 million eggs (Bull 1976).

After external fertilisation, the scallop larvae spend time in a planktonic form for 3–4 weeks, following which they settle to the seabed at metamorphosis (approx. 220 μm in size), attaching with byssus threads

to algae or other filamentous material (Bull 1976). Initial settlement requires suitable benthic substrate for byssal attachment to filamentous materials such as hydroids, bryozoans, algae, and seagrasses (Dredge et al. 2016). Such filamentous materials may keep scallop spat elevated above the seafloor and away from predators and unfavourable environmental conditions in and immediately above the benthos (Talman et al. 2004).

Once they have grown to approximately 5 mm, *P. novaezealandiae* will detach from their byssus and become free-living in the seabed sediment. Following seabed settlement, it can take 18 months to 3 years for scallops to reach harvestable size (90–100 mm) (Dredge et al. 2016). Although adult *P. novaezelandiae* can swim by clapping their valves, they are unable to move appreciable distances and do not appear to move much from their initial settlement location during their lifetime (Morrison 1999, Twist et al. 2016). As a result, morphological differences persist between adjacent sub-populations due to lack of population mixing (Fisheries New Zealand 2022). The high fecundity, and variability in the mortality of larvae and pre-recruits, is proposed to lead to a high variability in natural annual recruitment (Fisheries New Zealand 2022).

As with other species of scallop, habitat characteristics are proposed to be a structuring force determining *P. novaezealandiae* population abundance and survival. For example, scallops were found at higher densities with increasing distance from Paterson Inlet, Stewart Island. This is likely representative of changing habitat gradient or environmental variables (Twist et al. 2015).

Pecten novaezealandiae is found on a range of substrates, from silt to sand and gravel, but typically prefers sandy substrates. In Omaha Bay and Kawau Bay, northeast North Island, scallops are observed in greater densities on gravel, shell debris, and coarser grain sands (Morrison 1999, Taylor & Morrison 2008). In Paterson Inlet, Stewart Island, early benthic surveys revealed that scallops are primarily found on sandy and muddy bottoms, with individuals occasionally found on gravel substrate (Willan 1981). Coarser sediment environments, which tend to exist in areas with greater current speeds, generally have lower suspended sediment concentrations. These have been shown to disrupt feeding and growth processes in *P. novaezealandiae* due to a detrimental effect on ciliary activity, leading to increased adult mortality (Stevens 1987, Nicholls et al. 2003). As such, increased anthropogenic activity such as dredging and other environmental disturbances that increase turbidity and suspended sediment concentrations may affect scallop populations through increasing scallop mortality (Thrush et al. 1995).

Ecological interactions also play a key role in structuring *P. novaezealandiae* populations. Predation varies with scallop size, with spat and small juvenile scallops more vulnerable to predation generally and to a larger range of predators (Fisheries New Zealand 2022). As such, one of the main factors influencing juvenile scallop survival is predation (Talman et al. 2004). *Pecten novaezealandiae* predators include seastars (*Astropecten polyacanthus*, *Coscinasterias calamaria, Luidia varia*, and *Patiriella regularis*); fish including eagle rays (*Myliobatus tenuicaudatus*), stingrays (*Dasyatis* sp.), snapper (*Chrysophrys auratus*), tarakihi (*Nemadactylus macropterus*), and blue cod (*Parapercis colias*); hermit crabs (*Pagurus novaezelandiae*); and molluscs including octopus (*Macroctopus maorum, Pinnoctopus cordiformis*) and carnivorous gastropods (e.g., *Cominella adspersa*, *Alcithoe arabica*) (Bull 1976, Morrison 1999, Nesbit 1999, Ministry for Primary Industries 2013, Fisheries New Zealand 2022).

Habitat structure and complexity provides refuge from predation for juvenile scallops (Talman et al. 2004). As adult *P. novaezealandiae* have limited mobility, denser scallop populations are observed near complex habitats. These complex habitats can include fine filamentous material, such as algae, erect bryozoans, and other structures required for larval settlement and metamorphosis. However, not all habitat complexity is positively correlated with *P. novaezealandiae* abundance. For example, scallop abundance is negatively associated with mats of benthic macroalgae (Twist et al. 2016). This suggests that scallops could be removing or preventing settlement of macroalgal mats through their feeding activities, or that these mats are indicative of unfavourable scallop habitat (Twist et al. 2016).

Additional factors negatively associated with *P. novaezealandiae* populations include stressors such as weather events, harmful algal blooms, infection/disease, and anthropogenic pollutants. When exposed to dissolved metals and metal pollution, scallops accumulate trace metals in their tissues. *Pecten novaezealandiae* was found to accumulate elevated amounts of cadmium (in the viscera, digestive gland, gills, and adductor muscle), copper (in the digestive gland), and iron (in the gills), significantly above concentrations found in the surrounding environment (Peake et al. 2010). Infections by viral (Hine & Wesney 1997), prokaryote (Hine & Diggles 2002) and parasitic invertebrates such as the copepod *Pseudomyicola spinosus*, the polychaetes *Polydora hoplura* and *Chaetopterus* spp., and the flatworm *Paravortex* sp. (Woods & Hayden 1998), may also play a role in observed population declines. The flatworm *Paravortex* sp. was more frequently observed in gaping scallops, suggesting potential physiological effects (Woods & Hayden 1998). A previously unknown 'black gill' condition, which may have been caused by variations in seawater nitrate concentrations, salinity and La Niña weather patterns, was observed to decrease physical condition in Coromandel scallops during the summer of 1999–2000 (Smith & Diggles 1999). The incidence of harmful algal blooms is increasing worldwide, with environmental impacts and ongoing effects on marine ecosystems, fisheries, and aquaculture. Some of these blooms produce paralytic shellfish poisoning toxins. These can accumulate in scallop tissue (primarily in the digestive gland and were also shown to cause negative physiological effects on *P. novaezealandiae* feeding rates (Contreras et al. 2012a, b).

3. FIELD STUDY METHODS

3.1 Study design

We conducted a field study in Golden Bay and Tasman Bay at the north of New Zealand's South Island in 2018. The study involved deploying small juvenile scallops (spat) at a range of field sites in May 2018 and revisiting the sites in June and December 2018 to conduct dive sampling to provide data on scallop metrics and habitat variables for investigating scallop-habitat relationships. Analysis of the data collected enabled spat survival and growth to be examined in relation to the environmental and ecological variables measured at each site.

Field sites

Study sites were selected within areas known to have supported historically productive scallop beds, some of which were still productive at the time of the study, and that spanned a range of contrasting environmental conditions and habitats. Site selection was informed using data from past scallop surveys and using local ecological knowledge. Patterns in past scallop distribution were explored by mapping scallop density (the number of recruited scallops, 90 mm shell length or larger, per standard survey dredge tow distance of 0.4 n. miles) estimated using the 1994–2015 SCA 7 dredge survey data, normalised by survey year (Williams et al. 2015) (Figure 1). This analysis suggested the main scallop beds (highest densities of recruited scallops) in the past were generally found between 10 and 20 m depth in Golden Bay and between 15 and 25 m depth in Tasman Bay (Williams et al. 2015).

Ten sites were selected: Farewell, Puponga, Parapara, Patons, Wainui (Golden Bay sites) and Awaroa, Bark Bay, Adele, Motueka, and Croisilles (Tasman Bay sites) (Figure 1). The sites were spread across the SCA 7 scallop fishery reporting areas 7AA–7HH and were all considered to be historically productive scallop beds, encompassing sites well-known to commercial fishers, and in areas targeted by recreational fishers (Cole et al. 2006).

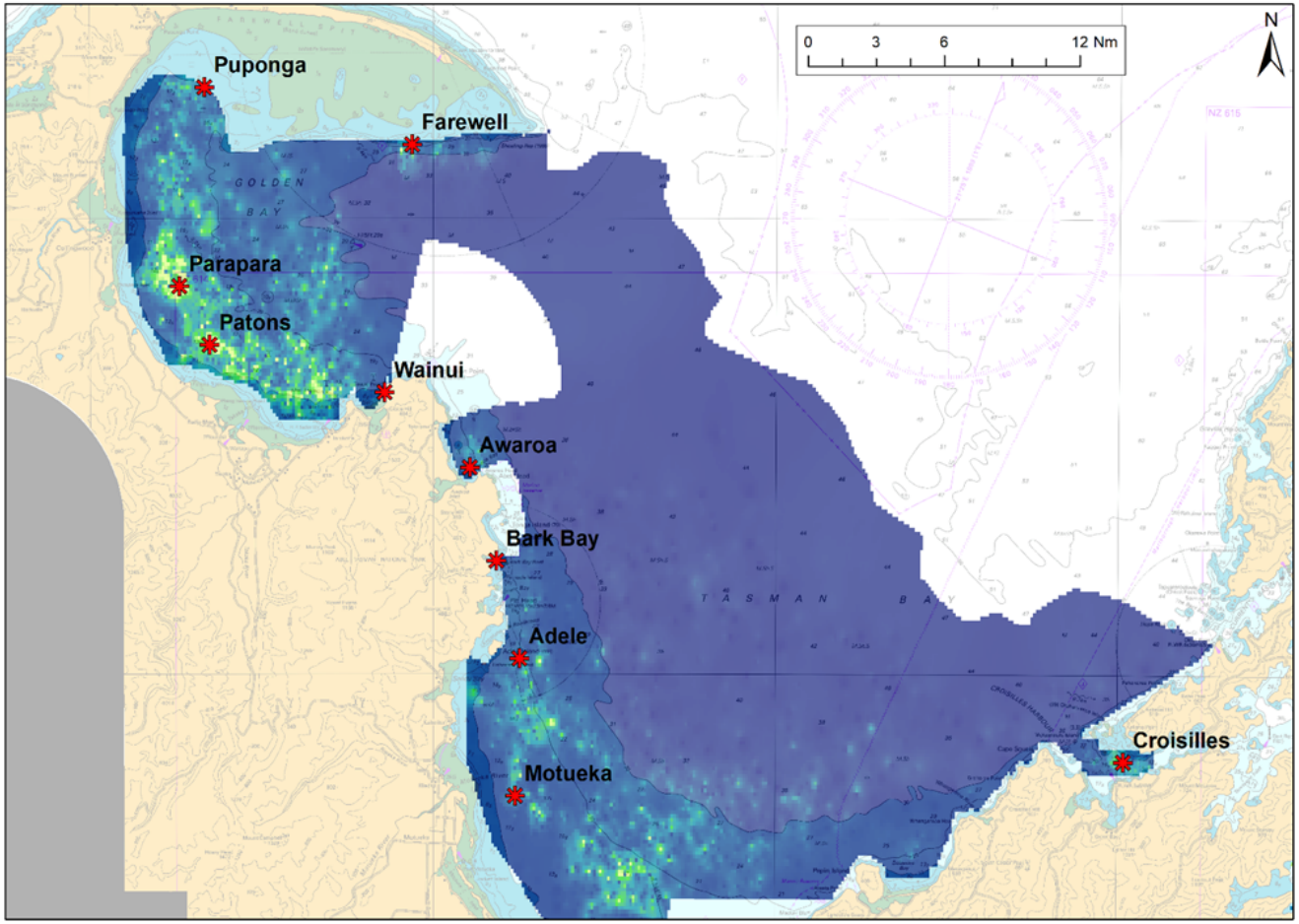

Figure 1: **Location of study sites (red symbols) where scallop spat were deployed in May 2018 and sampled by dive surveys in June and December 2018. The underlying coloured layer is an inverse density-weighted (IDW) interpolation of scallop spatial density estimated using the 1994–2015 SCA 7 dredge survey data (from Williams et al. 2015). Spatial density is the number of recruited scallops 90 mm or larger per standard survey tow distance (0.4 n. miles), normalised by survey year using standard score normalisation (observed minus the population mean divided by the population standard deviation). Colours transitioning from blue to green to yellow illustrate the historic distribution of scallop spatial density, showing low-density (blue), medium-density (green), and high-density areas (yellow).**

3.2 Scallop spat deployment methods

Spat source and health assessment

Scallop spat were sourced from Challenger Scallop Enhancement Company (CSEC), which operates a commercial spat catching site in Tasman Bay. Before commencing with the field study, the health of the spat was assessed by histopathology in early May 2018 (Webb 2018). No OIE (Office International des Epizooties – World Organisation for Animal Health) notifiable diseases or organisms were detected. Infection prevalence was determined for rickettsia type 1 and type 2, digestive epithelial virosis, mantle cavity copepods, vermiform gregarine, and kidney concretions. The parasites and pathogens encountered were typical of scallop populations and did not give cause for concern. All conditions detected in the spat examined are typical scallop parasites and have been noted previously at high levels in scallops from Marlborough Sounds and elsewhere. Many of the histological sections showed minor structural disruption that may be associated with cold temperature stress.

Spat marking

Spat marking work for the field study was conducted on 17 May 2018 on board the barge *Tui* during CSEC's spat harvesting operations at their spat catching site in Tasman Bay. Spat collector bags attached to dropper lines were hauled onto the barge and removed from the lines. Each bag contained hundreds to thousands of scallop spat (and other associated fauna that were present inside the bags). The bags were processed by a team of workers: the bags were cut open and the spat were shaken out into large bins. A single bin of spat was selected at random as the source of spat for the field study.

Spat used in the field study were marked with calcein. Calcein is a fluorochrome dye compound that binds with earth metals in suspension resulting in an increase in fluorescence (Lucas et al. 2005, Spires & North 2022). Calcein labelling offers a rapid non-invasive method for mass marking of juvenile bivalves (Spires & North 2022). This marking allows tracking of released spat populations and can be used to record growth. We had intended to investigate the utility of marking for determining the origin of the scallops (i.e., naturally settled or enhanced) to aid in our examination of survivorship, and to use the calcein marks for investigating patterns in individual shell growth by measuring the increment from the calcein ring to the edge of the shell. However, the success of marking was variable: although definitive marks were visible in the external appearance of some shells (Figure 2), the marks were patchy or difficult to detect in other shells. Preliminary thin sectioning of shells revealed marks were present but, due to project resources, further investigation using sectioning was not feasible. Nevertheless, spat marking methods are described here because they potentially could have affected the vitality of the spat released.

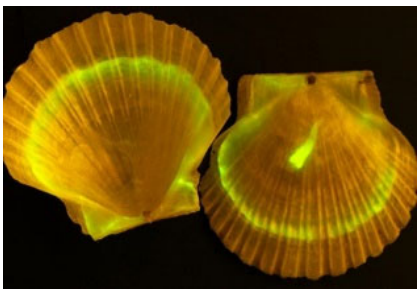

Figure 2: Example photo of scallop shell valves marked with the fluorescent calcein. Photo by C. Ó Maolagáin (NIWA).

The scallop enhancement process (recovery from spat collection facilities and redeployment) is thought to leave a visible shock ring (or check mark) in the shell, and so all recovered scallops were examined and categorised as being with or without visible check marks. However, it should be noted that the check mark may be caused by other forms of shock in addition to enhancement, and we cannot confirm that all spat with a check mark were enhanced. This could have been investigated through examination of the calcein stain mark, but this was not possible within the project resources.

Scallop spat (7–52 mm shell length; mean = 22 mm) were placed in new green mesh spat bags, with two standardised scoops of spat per bag (~150 spat per bag), bundled in sets of four bags. In total, 143 sets (572 bags or ~85 800 spat) were marked with calcein (3 h immersion in 150 mg L^{-1} solution of calcein in seawater), and 12 sets (48 bags or 7200 spat) were unmarked controls (3 h immersion in seawater). After the marking treatments, the mesh bags were cable-tied to dropper lines attached to a main backbone line at the spat-catching site, for retrieval later in May 2018 for use in the spat deployment phase of the field study.

Spat sampling for initial mortality before release

To estimate the number of live spat released at each location, random samples of spat bags from the calcein and control marking treatments were taken and examined by counting the number of live and dead spat in the samples.

On 17 May 2018, before the bags were deployed on the dropper lines, samples of calcein-marked and unmarked (control) spat (n = 5 per treatment) were randomly selected for initial mortality sampling. The contents of each bag were examined on a sorting tray: any dead spat (gaping valves, hinge still attached) were separated from the live spat and other species present, and these dead and live subsamples were individually bagged and retained inside one main labelled sample bag per spat bag. Samples were processed in the laboratory, by counting and measuring the size (shell length, in mm, the longest dimension parallel with the shell hinge) of dead and live spat to determine the proportion already dead at the time of marking, and to characterise spat size frequency. After this initial mortality sampling, 566 calcein bags and 42 control bags remained and were deployed on the dropper lines.

The 17 May 2018 mortality sampling process was repeated on 28 May 2018 when conducting the site deployments. This was done by randomly selecting 6 bags of calcein-marked and 6 bags of unmarked spat, sorting live from dead spat in each bag, and retaining these in labelled bags for later analysis in the laboratory.

After the 28 May spat mortality sampling, in total there were 560 bags (i.e., 140 sets of four bags) of calcein-marked spat available for the field study, equating to 56 bags (i.e., 14 sets of four bags, or ~8400 spat) available for deployment at each of the ten study sites. The remaining 36 bags of control spat were not used in the field study.

Spat retrieval and release

On 28 May 2018, half of the sets of bags containing marked spat were transferred from the line and into large tanks (0.6 m^3) of flowing seawater on the vessel *Adele II* for transfer to the Tasman Bay sites (ambient temperature and high levels of oxygen were maintained during transit). The remaining sets of bags were transferred to the Golden Bay sites on 29 May 2018. Spat exposure to air (emersion from water) was minimised. The sets of control bags were also removed on 29 May but were not used in the field study.

The 10 field sites were in depths shallower than 25 m. At each site, a weighted mooring line with surface marker buoy was deployed to mark the centre of a single 30 m × 30 m (900 m^2) seabed plot. The dropper bags were deployed from the surface to within about 3 m of the seabed and opened remotely using a release rope; bags of spat were deployed at approximately 10 m intervals in a 3 × 3 grid (centred on the site marker buoy) with the goal of releasing 9 bags per square metre across the plot (Figure 3), although wind and current conditions meant that this was not always possible. Total numbers and density of spat released at each site were estimated based on the number of bags deployed, and an average of 114.7 live spat per bag (Table 1). Uncertainty in spat dispersal to the seabed in relation to prevailing currents may have resulted in lower spat densities landing within each seabed plot.

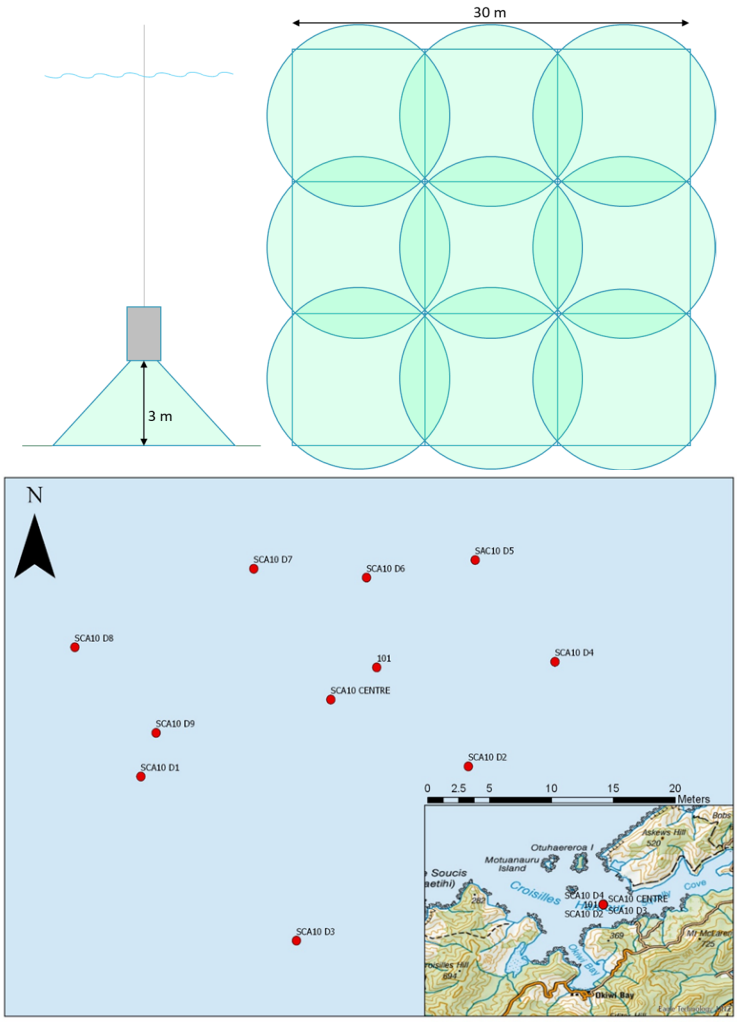

Figure 3: **Schematic and example map of scallop spat release, May 2018. Top: Spat were released from bags held 3 m above the seafloor in a 3 × 3 grid over a targeted 30 m × 30 m area. Bottom: Example map showing actual spat release positions at the Croisilles Harbour site.**

Table 1: **Summary of spat bags used during deployments of spat released at sites in Tasman Bay (28 May 2018) and Golden Bay (29 May 2018). The approximate number and density of spat (spat per square metre) per site were calculated assuming an average of 115 live spat per bag (see results in Section 4) and a release plot area of 900 m^2.**

Bay	Site	Depth (m)	Deployments	Bags	Spat number	Density (spat m^{-2})
Golden Bay	Farewell	12	9	51	5 853	6.50
	Puponga	15	10	56	6 427	7.14
	Parapara	16	10	57	6 542	7.27
	Patons	16	10	52	5 968	6.63
	Wainui	9	10	50	5 739	6.38
Tasman Bay	Awaroa	20	10	55	6 312	7.01
	Bark	9	10	50	5 739	6.38
	Adele	21	10	51	5 853	6.50
	Motueka	15	9	51	5 853	6.50
	Croisilles	15	10	64	7 345	8.16
			Totals	*98*	*537*	*61 633*	*Overall mean: 6.85*

3.3 Data collection methods

Field data on scallops and the environmental characteristics and ecological communities at each site were collected by conducting two dive survey trips, during 16–20 June 2018 (first sampling time point) and 4–11 December 2018 (second sampling time point). On each trip and at each site, dive sampling involved two scuba divers conducting quadrat sampling to collect scallops, benthic samples and measurements, and seawater samples. Topside sampling from aboard the survey vessel involved deploying an oceanographic instruments package and conducting towed video camera transects. Data collection methods are summarised in Table 2 and described below in greater detail and apply to each site and sampling time point. Note that at the first sampling time point in June 2018 it was not possible to locate the site mooring for the Adele site in Tasman Bay, and so sampling at that site was abandoned. An additional site, Croisilles 2, which supported a healthy scallop bed in Croisilles Harbour, was opportunistically sampled at the second sampling time point in December 2018.

Scallop sampling

The scallop population at each site was sampled by searching for and collecting scallops within quadrats spaced at fixed distances along transects that extended out from the central site mooring across the spat release plot. The aim of this sampling design was to ensure that the sample of quadrats (target of n = 8–12 per site) fell within and was representative of the area of the seabed over which the spat had been released in May 2018. Due to differences in the prevailing tidal currents at each site during the spat release deployments, the overall release plot area varied among sites. To account for this, the number of transects required (n = 2–4), transect bearings (i.e., taken from the central site mooring), transect distances (10–40 m), and quadrat spacings (5 or 10 m) were predetermined for each site using information on the spat release positions recorded during the May 2018 deployments. Due to time constraints in the field, sampling at each site had to be completed during a single dive. At each site, the same quadrat and transect sampling design as used in June was repeated in December 2018. In addition, in December 2018, scallops encountered along the transects but outside the sampled quadrats were also collected and bagged separately, to boost the sample size of scallops available for investigating scallop condition and disease.

For example, sampling at the Wainui site was designed to match the spat release plot by using a cruciform arrangement of four 15-m transects, each laid out in turn from the central site mooring on the four cardinal bearings (0°, 90°, 180°, 270°). On each transect, two quadrats were searched at predetermined fixed distances of 5 and 15 m from the central site mooring. For each transect, the divers attached the end of the transect tape to the bottom of the site mooring and swam out the transect tape according to the predetermined bearing (e.g., north, 0°) and distance (15 m). The divers positioned themselves on either side of the transect at the 15-m mark on the tape and commenced a quadrat search for scallops. The quadrat search involved the two divers, each holding a 1.2-m wide bar on their side of the transect line, collecting all scallops found under the bar along a 2-m length of the transect (i.e., from 15 m to 13 m on the transect tape: 1.2 m × 2 m × 2 divers = 4.8 m^2 overall area searched per quadrat). All scallops found within the quadrat were placed into a sealed labelled bag, stored within a catch bag. A subsequent quadrat search was conducted at the 5-m predetermined fixed distance along the transect. This quadrat sampling process was repeated along transects on the remaining three transect bearings (total of n = 8 quadrats sampled at Wainui in June 2018). Video footage was recorded using mask-mounted GoPro cameras worn by the divers.

After the dive, scallop samples were frozen (June 2018 sampling) or held on ice (December 2018 sampling, to facilitate histopathology studies). At the laboratory, scallops were processed to provide data on scallop life status (live or dead) and size (shell length, in mm, measured using digital vernier callipers). Some spat recovered in June were found attached together in clumps, bound by the byssus threads of green-lipped mussels *Perna canaliculus* (that likely initially settled in the spat bag collector bags with the scallop spat), so each scallop recovered from the dive sampling was categorised as being free-living or attached. Each scallop recovered was also examined for the presence or absence of a check mark in the shell and categorised as being with or without a check mark.

Table 2: Summary of field sampling methods used in June and December 2018 to obtain the target data for analysis. *n*, target sample size per site on each sampling date. * indicates data that were not analysed for this report. ^Towcam video transects were conducted in December 2018 only.

Sampling method	*n*	Target data for analysis	Sample processing details
In situ mooring			
Oceanographic instruments package (ADCP and CTD)	1	Current velocity and direction, salinity, temperature, depth, dissolved oxygen, turbidity, chlorophyll *a*.	Data logged *in situ* for the duration of field sampling at each site.
Dive sampling			
Seawater samples (at 5 m, 1 m, and 0 m above seabed)	3	Dissolved oxygen (DO), turbidity, total suspended solids, particulate carbon and nitrogen, chlorophyll *a*.	Dissolved oxygen (DO) measured immediately post-dive using an optical DO probe. Seawater samples transferred to labelled bottles stored on ice in the dark. Seawater subsample filtered immediately post-dive and filters frozen. Seawater samples and filters shipped to water quality laboratory for analysis.
Quadrat searches (4.8 m^2) at fixed distances along transects spanning the study site	9–12	Scallop numbers, length, and life status (live/dead), used for estimating scallop density and length frequency, spat survival and growth. Shell and tissue weights for estimating condition. Tissue histology for investigating disease.	Scallops from each quadrat bagged and frozen and processed in the laboratory (scallop measurements and weights). For histopathology studies, scallop samples collected in December 2018 were held on ice (not frozen) before processing and preserving tissues for histological sectioning.
Sediment scrapes	4	Sediment particle size, organic matter, chlorophyll *a*, phaeopigment content.	Sediment pottles labelled, bagged and frozen for laboratory processing.
Sediment measurements	4	Sediment softness and compressibility.	Ruler and penetrometer measurements recorded on diver wet notes during the dive.
Benthic cores	4	Macrofaunal abundance, community, and diversity.	Cores sieved on 0.5-mm mesh and preserved in 70% isopropyl alcohol in 1-L jars). Samples sorted and identified in the laboratory.
Dive computers	2	Depth.	Maximum depths recorded on dive log.
Diver mask-mounted GoPro video camera*	1	Record of diver sampling.	Video files saved to hard drives during each trip and archived post-trip.
From survey vessel			
Secchi disc	3	Sea surface vertical water clarity.	Secchi readings taken from aboard the vessel whilst dive sampling was underway at each site.
Towcam video transects^	3	Counts of large epifauna (e.g., invertebrate predators/competitors) and benthic features.	Video analysed in the laboratory.

Scallops from the December 2018 sampling were dissected and weighed to provide body condition data. First, following the measurement of shell size, the total wet weight (recorded to the nearest 0.1 g) of each scallop was weighed and recorded. The scallop was then dissected to remove all soft tissue from the two shell valves, and the two components (soft tissue and shell) were blotted dry on paper towels and weighed. For adult scallops of reproductive size (70 mm or larger), soft tissue was further dissected into three constituent body parts (gonad, muscle, viscera) and each were individually blotted and weighed. For each scallop, the soft tissues were preserved in 10% buffered formalin and the shells were retained in labelled bags stored frozen in the dark.

For investigating scallop disease (pathogens and parasites), a subsample of scallops (n = 98) collected in December 2018 was selected and their preserved tissues were sent to Massey University for embedding in paraffin wax and sectioning (single section through the whole combined soft tissue, or through the three constituent body parts, ideally sectioning all body tissues of interest) to produce one histology slide per scallop. Slides were screened by a histopathologist at MPI's Animal Health Laboratory (AHL) in Wellington. Summary information from the AHL report received is provided in Appendix 1.

Environmental sampling

An oceanographic instruments package was deployed from the vessel to log data on properties of the water column at each site. The package consisted of an Acoustic Doppler Current Profiler (ADCP) and a Conductivity-Temperature-Depth (CTD) sonde attached to a weighted steel frame. The ADCP (Nortek 'Aquadopp') measured water current flow velocities in depth bins from the sea surface to the seafloor using the speed of sound echoes returned from particles present in the water column. The CTD (YSI EXO1 Multiparameter Sonde; https://www.ysi.com/exo1) was configured with sensors that measured seawater salinity (conductivity) and temperature, depth (pressure), dissolved oxygen, turbidity, and total algae (chlorophyll *a* plus blue green algae – phycocyanin). On arrival at each study site the instrument package was gently lowered to the seafloor about 50 m 'upstream' of the site before dive sampling commenced, to ensure the water parameter data logged were unaffected by the divers potentially stirring up sediments from the seabed. After completing the required dive sampling at each site, the package was retrieved and the logged data were downloaded. When feasible, the package was left *in situ* overnight to log data through a full tidal cycle.

Divers collected all other environmental data and samples. Water depth was measured at each site using a dive computer (Perdix Shearwater) strapped to each diver's wrist. Depth data were later corrected to Lowest Astronomical Tide. From the survey vessel, Secchi disc readings of vertical water clarity were taken whilst the dive sampling was underway.

Surficial sediment samples (n = 4 replicate ~30 g scrapes to 2 cm depth collected using 70 mL pottles) were taken to characterise sediment particle size distribution, organic matter content (OM), chlorophyll *a* content (Chl *a*), and phaeopigment (Phaeo) content. This sediment sampling deliberately targeted the seabed surface sediments which scallops inhabit and directly interact with, sediments that are likely the most vulnerable to being resuspended in the water column. The sediment samples were collected at haphazard positions situated ~5 m away from the site mooring, on each of the four cardinal bearings (0°, 90°, 180°, 270°). After collection, all sediment samples were kept cool and in the dark and were frozen on the survey vessel as soon as practicable. For analysis, sediment samples for particle size distribution (% by weight in different size categories) were thawed, homogenised, and digested in 9% hydrogen peroxide to remove organic matter that can cause particles to stick together (Greenfield et al. 2019). Samples were then wet sieved across a set of nested sieves (63, 125, 250, 500, 1000, and 2000 µm). Pipette analysis (based on differential settling rates of fine particles) was used to determine 3.9–63 µm silt and 0–3.9 µm clay fractions. Sediment organic matter content was determined on a separate 5-g subsample that was homogenised and dried to a constant weight in an oven at 60 °C. Organic matter content was determined as dry sediment mass lost following ignition after combustion in a muffle furnace at 400 °C (Greenfield et al. 2019). Sediment Chl *a* and Phaeo (µg g^{-1}) were determined spectrophotometrically following extraction in 95% ethanol (Greenfield et al. 2019).

Sediment measurements were also taken at haphazard positions situated 5 m away from the site mooring to further characterise the physical nature of the seabed. Sediment softness was estimated by taking four replicate measurements of the vertical penetration depth (mm) of a weighted metal ruler (30-cm stainless steel ruler with a 1-kg lead weight attached at the far end) placed perpendicular to the sediment surface and left to sink under its own weight. Sediment compressibility was measured by taking four replicate measurements with a handheld soil penetrometer (6.25 inch /158.8 mm spring-operated device which measures compressive strength in kg cm^{-2} by pushing a loading piston, with attached 36 mm diameter foot, into the sediment to a depth of 0.25 inches / 6.4 mm).

Seawater samples (3 × 1 L collected using sealed containers) were taken at each of 5 m, 1 m, and 0 m above the seabed. These samples were collected during the diver's descent to the seabed at the start of each dive, to avoid the possibility of the dive sampling stirring up sediments and affecting seawater parameters. Immediately post-dive, the level of dissolved oxygen (DO) in each sample was measured using a calibrated hand-held optical-based DO sensing meter (YSI). From each seawater sample, a subsample (300 mL) was filtered (25 mm GF/C filter) and the filter was frozen (-18 °C) for chlorophyll *a* analysis (mg m^{-3}, acetone pigment extraction, spectrofluorometric measurement). The remainder of each seawater sample was transferred to a labelled bottle and stored in the dark on ice for transfer to the onshore laboratory for analysis of turbidity (NTU, turbidimeter rated against Formazin standards), total suspended solids (g m^{-3}, filtration, drying at 104 °C, followed by furnacing at 400 °C), and particulate carbon and nitrogen (mg m^{-3}, catalytic combustion at 900 °C, sep, TCD, Elementar C/N analyser).

Ecological sampling

Benthic macrofauna

To provide information on macrofaunal communities present at each scallop survey site, four benthic sediment cores (10-cm internal diameter × 16-cm depth) were collected haphazardly within 5 m of the site mooring. Sediment cores were sieved across a 0.5 mm mesh screen and preserved in the field with 70% isopropyl alcohol. At the laboratory, Rose Bengal was added to each sample to stain all biological material red to facilitate the sorting of macrofauna from sediment and shell debris. After sorting, all macrofaunal individuals were identified to the lowest practicable taxonomic level and enumerated. This yielded data on the abundance of individual macrofauna taxa (e.g., *Euchone pallida*, Exogoninae, *Macroclymenella stewartensis*) and on characteristics of the macrofaunal community as a whole (e.g., total number of individuals per core (i.e., abundance, N), number of macrofauna taxa per core (i.e., richness, S), and macrofaunal diversity (Shannon-Wiener H' index). All ecological descriptors were calculated using PRIMER software.

Large epifauna

Three benthic video transects (mean transect length = 60 m, range = 23–133 m; mean width = 0.53 m, range = 0.37–0.92 m) were conducted across the spat release plot at each study site in December 2018 using a drop-towed digital video camera system ('towcam'), and the footage was examined to obtain counts of large epifauna and the presence of benthic features per transect. Counts were converted to densities per square metre using the estimated area swept by the camera (transect length × mean image width). Poor visibility prevented quantification of benthic fauna at Motueka and Parapara, but visible species (or groups) were identified and counted at other sites, and habitat features were identified at all sites.

Additional towcam video sampling was conducted during the December 2018 trip to explore for potential scallop beds located outside the study sites based on anecdotal information (Figure 4).

Figure 4: Map of towcam video transect sampling positions, December 2018. Stars indicate study site locations. Triangles and numbers indicate the locations of exploratory towcam sampling outside of the study sites.

3.4 Data and statistical analysis methods

Scallop spat data analysis

Analysis of deviance was used to test for the effect of treatment and date on the proportion of dead spat in the sample bags from May. A kernel density estimate (KDE) test (Langlois et al. 2012) was used to determine the difference in the length composition of live and dead spat between the two dates and treatments (control vs. calcein marked).

For each site and dive sampling event (June and December), data on the number and size (shell length) of live free-living scallops recovered during the quadrat sampling (i.e., data summed across all quadrats sampled per sampling event) were examined to determine scallop length frequency, median scallop length, and mean scallop density. Scallops attached together, bound by the byssus threads of mussels and other scallop spat, were excluded from the analysis. For each site, mean scallop density estimates were used to calculate relative survival estimates between the different pairs of May, June, and December sampling time points (i.e., $density_2$ / $density_1$), and median scallop length estimates were used to calculate absolute ($length_2$ − $length_1$) and relative ([$length_2$ − $length_1$] / $length_1$) growth increments between the different pairs of May, June, and December sampling time points.

The relationship between scallop tissue weight (sum of gonad, muscle, and viscera blotted wet weights) and shell length was modelled using linear regression (fitting to log-transformed data for all scallops less than 80-mm shell length, with the sample comprised of scallops recovered from within quadrats plus those 'extra' scallops collected from outside the quadrats), and standardised residuals for each observation were examined for patterns among sites.

Environmental and ecological data analysis

ADCP/CTD data were processed to provide the 95th percentile of the maximum current speed (which acts to filter out erroneous high magnitude spikes in the data). Environmental correlations were visualised using corrplot (Wei & Simko 2021) and boxplots in R.

Principal component analysis (PCA) was used in the data exploration to examine the ordination of sites relative to environmental variables, to identify any strong environmental gradients. Pairwise scatterplots and correlation coefficients between explanatory variables were examined to check for collinearity (the existence of correlation between covariates), and, when high correlations were identified, some variables were excluded from the subsequent analysis.

Multivariate analysis of the video transect fauna and benthic core macrofaunal community data was conducted using PRIMER. Numbers of individuals per species or taxonomic group within each sample were standardised and square root transformed before a Bray-Curtis similarity matrix was used to generate a non-metric multi-dimensional scaling (MDS) plot. MDS of the benthic community data provides a preliminary examination of the spread of sites across ordination space and can be used to identify the relative similarity/dissimilarity of sites based on their multivariate community data. Where differences in community composition show a good spread in ordination space, rather than being driven by a few distinctly different sites or clusters, analyses of drivers of community composition using continuous variables is likely to be robust.

Determining environmental indicators of habitat suitability

To determine the effect of environmental conditions on scallop spat, the scallop density, survival, and growth estimates from each of the study sites were examined in relation to the environmental drivers within a generalised linear modelling framework to determine the strongest drivers. Several environmental variables were strongly correlated with each other (correlation coefficients ≥ 0.7 or ≤ -0.7), so some were excluded from statistical models to avoid variance inflation. Models were constructed to test the effect of environmental explanatory variables on the scallop response variables of survival, density, and growth.

Relative growth was estimated from the median size of released spat in May and the median size of recovered juvenile scallops (smaller than 80 mm) in December. Relative growth was expressed as the increase in median size divided by the median size at release. Scallop survival estimates used in the modelling were calculated from the June and December estimates of scallop density derived from the diver quadrat sampling. Scallop density in December 2018 was considered a proxy for scallop survival and enabled inclusion of data from the Farewell and Croisilles 2 sites (the survival estimate for Farewell was considered unreliable and was excluded due to the higher mean scallop density in December; a survival estimate for Croisilles 2 was not possible because this site was not initially included in the study and was sampled only once, in December).

An initial model was fitted to the response variable, with explanatory variables of sediment chlorophyll *a*, sediment phaeopigment, sediment % mud, sediment % gravel, depth, seawater dissolved oxygen, seawater particulate carbon, and seawater chlorophyll. Subsequently, a stepwise model selection procedure was used which dropped terms in a backwards and forwards stepwise process using the *step* function in R to select the model with the smallest AIC.

For the three scallop response variables, model selection was run with and without depth; while depth varied between sites and influences benthic conditions for scallops, all the sites examined have supported scallop populations in the past, and this variable remains unchanged over time.

4. FIELD STUDY RESULTS

4.1 Scallop spat monitoring

Scallop spat marked in May 2018

Given time constraints, scallop spat were not examined individually, and some were dead before the spat deployments were conducted. The proportion dead was analysed in relation to treatment and sampling date within a binomial generalised linear model. There was no significant effect of treatment, date, or an interaction between the terms, on the proportion of dead spat (Table 3). Across the two treatments there was no difference in the proportion dead by date (Figure 5), and across the two dates there was no difference by treatment (control vs. calcein marked; Figure 6). The individual date treatment combinations showed more variability (Figure 7) but the interaction term was not significant (P = 0.4). Across all samples, 11% of scallop spat within the sample bags were dead, and bags contained an average of 115 live spat (95% Confidence Interval (CI) 67 to 154). We can conclude that the spat staining process had no effect of the health or mortality rate of the spat.

Table 3: Analysis of deviance table for model examining effect of treatment and date on proportion of dead spat in sample bags.

	Df	Deviance	Res Df	Res Dev	P (Chisq)
NULL			21	25.270	
treat	1	0.20330	20	25.067	0.65
date	1	0.28580	19	24.781	0.59
treat:date	1	0.70938	18	23.072	0.40

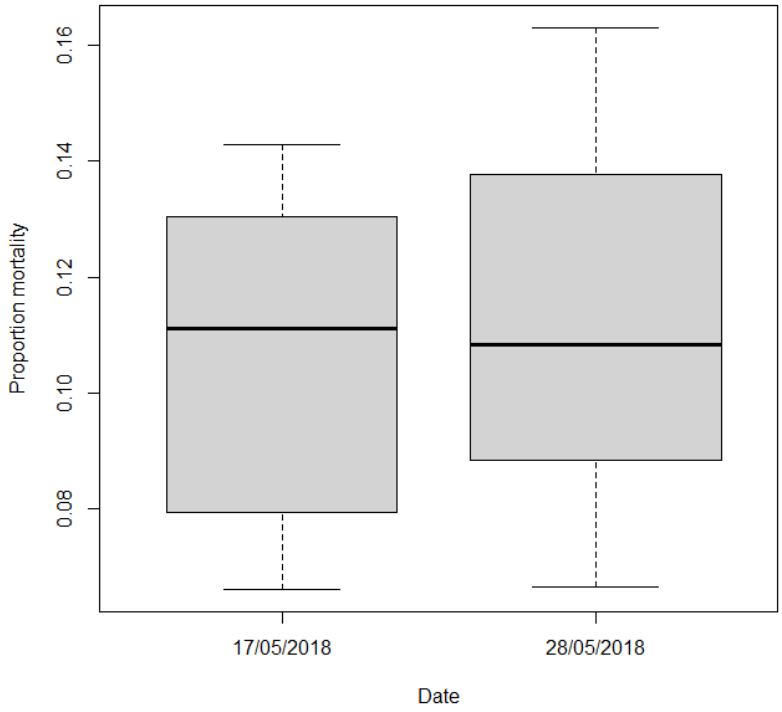

Figure 5: Boxplot of proportion mortality in the spat samples by sampling date (combined across treatments).

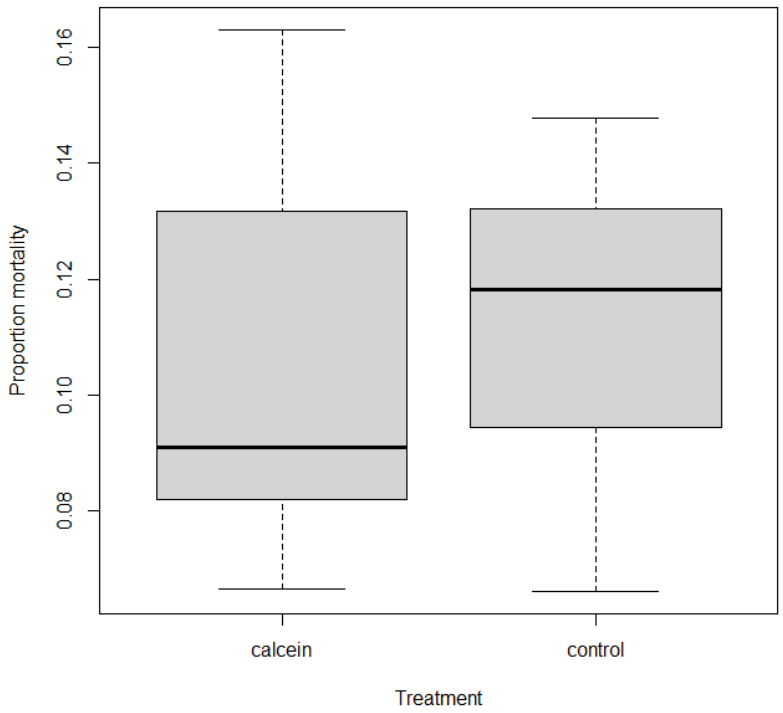

Figure 6: Boxplot of proportion mortality in the spat samples by treatment (combined across sampling dates).

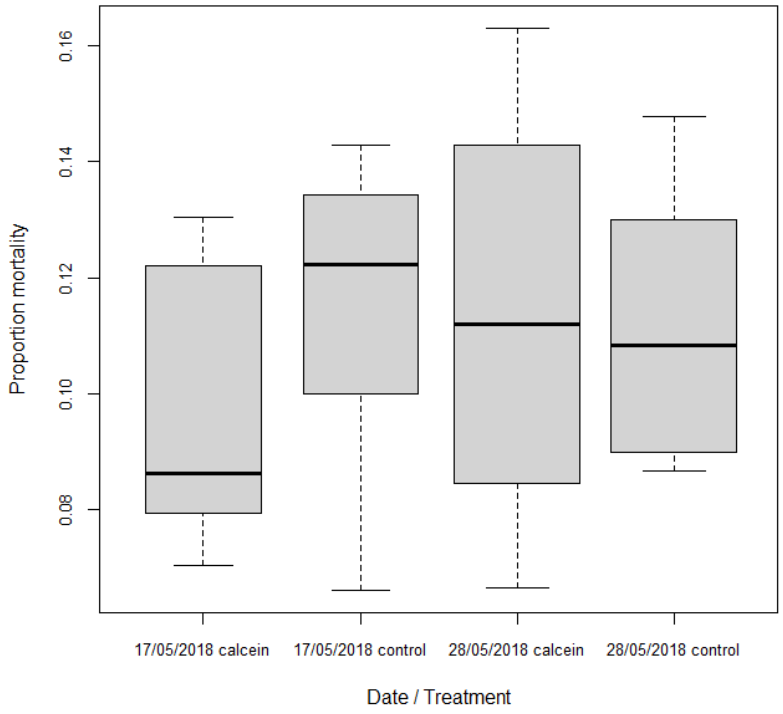

Figure 7: Boxplot of proportion mortality in the spat samples by sampling date and treatment.

Scallop spat characteristics at the time of release in May 2018

There was no significant difference (kernel density estimate test, KDE; Langlois et al. 2012) between the shell length of the live vs. the dead spat (Figure 8) or between live calcein-treated scallops in the sampled bags between 17 and 28 May 2018 (Figure 9).

The shell length structure of the live scallops at the time of release was estimated from the combined scallop samples. Confidence intervals were estimated from 100 resamples (with replacement) of the 22 separate samples of data available from the 17 May 2018 (n = 10) and 28 May 2018 (n = 12) initial mortality sampling. Spat shell length ranged from 7 to 52 mm, and half of the spat had a shell length between 16 and 27 mm (mean = 22.4 mm; median = 21.3 mm) (Figure 10).

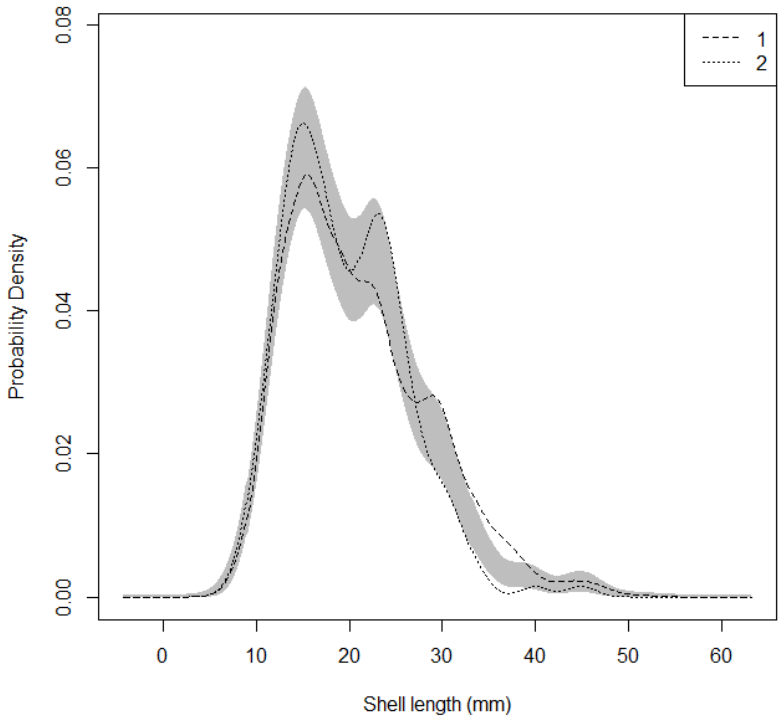

Figure 8: Comparison of kernel density estimate (KDE) probability density functions (using mean bandwidth as the smoothing parameter) for the shell length of live and dead scallop spat within sampled bags. Dashed and dotted lines represent live (1) and dead (2) spat, respectively. The grey shaded band represents one standard error either side of the null model of no difference between the pair of KDEs.

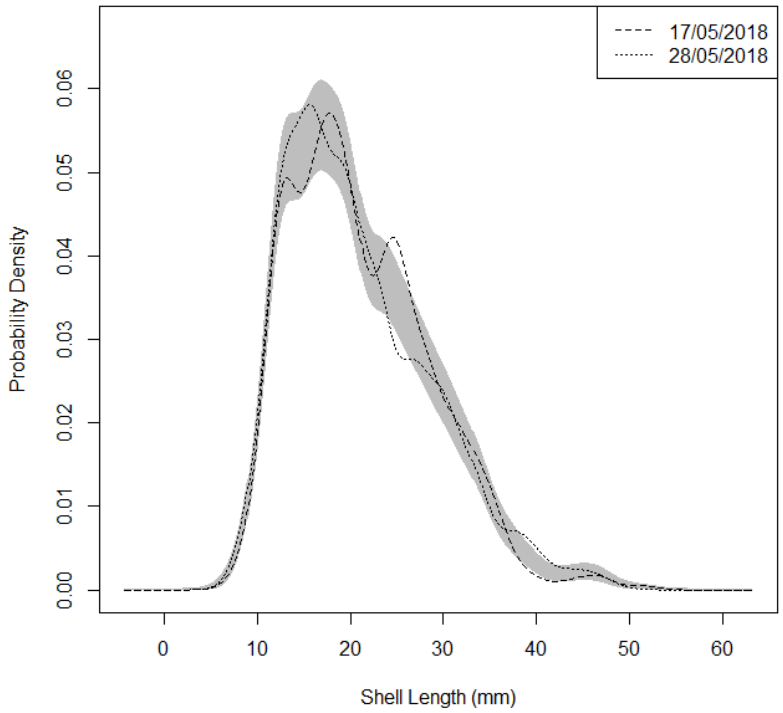

Figure 9: Comparison of kernel density estimate (KDE) probability density functions (using mean bandwidth as the smoothing parameter) for the shell length of live scallop spat on 17 and 28 May 2018. Dashed and dotted lines represent the first (17/05/18) and second (28/05/18) sampling dates, respectively. The grey shaded band represents one standard error either side of the null model of no difference between the pair of KDEs.

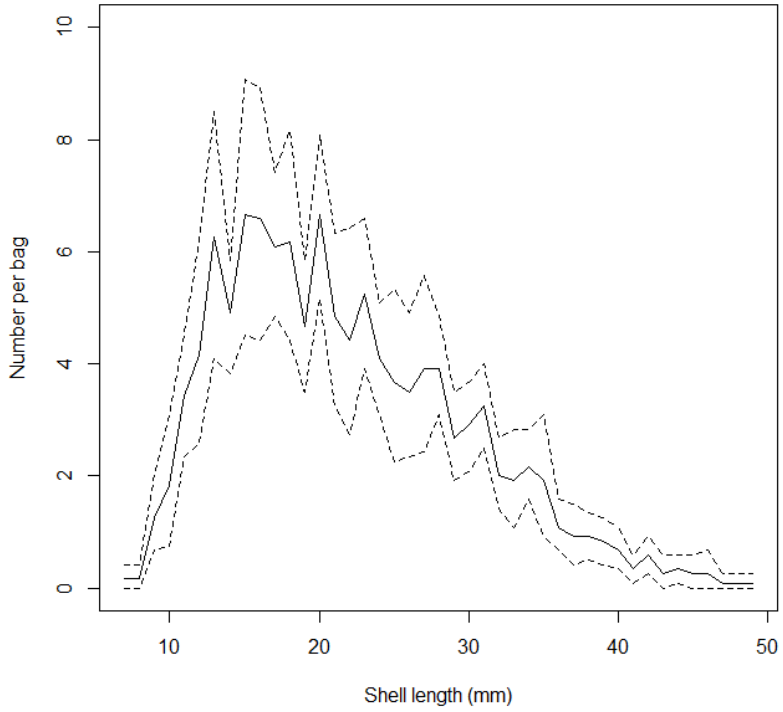

Figure 10: Estimated scaled shell length frequency (numbers of scallop spat) per bag. Solid line represents mean estimate, with dashed lines representing 95% confidence intervals.

Scallop length frequency and density estimates in June 2018

In the survey design, the target was for divers to sample a total of eight to twelve quadrats along transects that spanned the release plot at each site. However, only between four and nine quadrats were able to be successfully sampled at each site in June 2018 (see Table 4). This variation was due to the time constraint of needing to complete all sampling at a site during a single dive, and because of poor underwater visibility at some sites which increased the search time required per quadrat. Sampling was not possible at the Adele site due to a missing marker buoy, and further study at this site had to be abandoned.

The length frequency distribution of all live scallops recovered from the sampled quadrats in June 2018 shows two distinct length modes, one between 10 and 50 mm, and one between 70 and 100 mm (Figure 11). Not all scallops recovered during the dive sampling would have originated from our experimental release. Some may have settled naturally in 2018, and others (we assume all greater than 60 mm) would have settled naturally in previous years. Examination of changes in scallop density over time have been conducted on the full population of free-living live scallops. For scallops smaller than 60 mm in June 2018, scallop shell length in June 2018 ranged from 8 to 58 mm, and half of the scallops had a shell length between 21 and 34 mm (mean = 28.1 mm; median = 27.2 mm) (Figure 11).

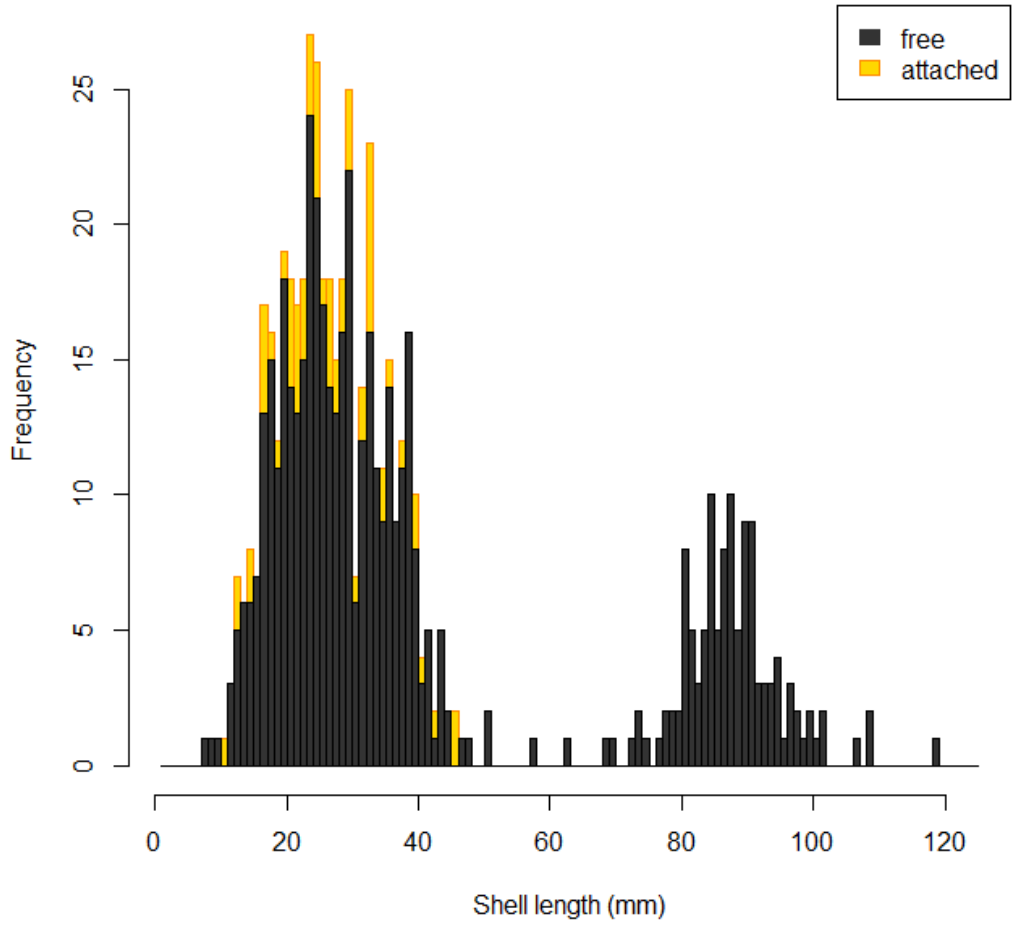

Figure 11: Length frequency distribution of all live scallops recovered from sampled quadrats across all sites in June 2018. Bar colour distinguishes free-living scallops (black) from those byssally attached in clumps (yellow); the latter were excluded from the analysis.

The June 2018 individual site length frequency distributions show that the scallops recovered from each site fell within the two distinct length modes observed in the overall length frequency distribution: 10–50 mm and 70–100 mm (Figure 12). Scallops greater than 60 mm in length were observed only at four sites: Farewell, Croisilles, Wainui, and Bark (Figure 12). At Parapara, Motueka, Awaroa, Patons, and Puponga, only smaller (presumed released) scallops were recovered (Figure 12).

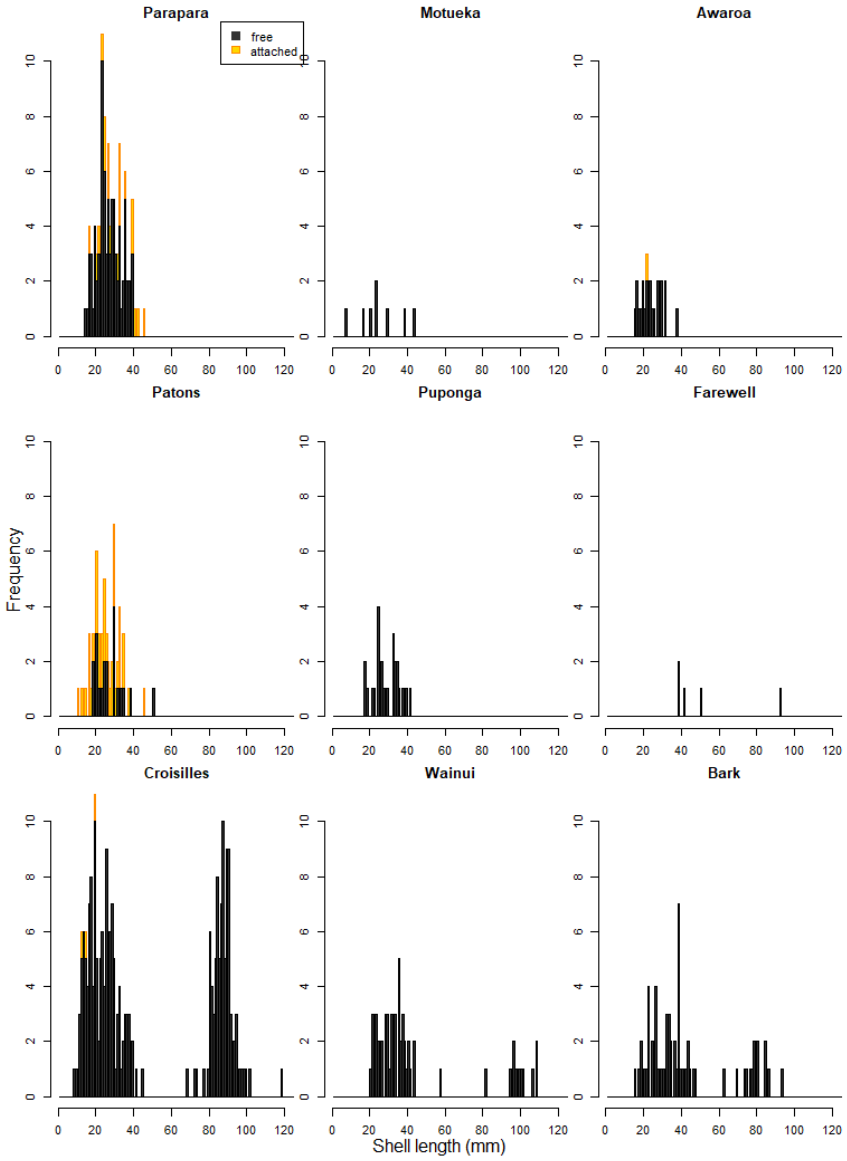

Figure 12: Length frequency distribution of live scallops recovered from sites in Golden Bay (Farewell, Puponga, Parapara, Patons, and Wainui) and Tasman Bay (Awaroa, Bark, Motueka, and Croisilles) in June 2018. Bar colour distinguishes free-living scallops (black) from those byssally attached in clumps (yellow). Note levels of sampling varied among sites (Table 4). Sites are ordered from top left to bottom right with increasing scallop density (scallops < 80 mm m^{-2} in December 2018) (see Table 5).

A total of 389 live free-living scallops smaller than 60 mm were recovered from the 64 quadrats sampled in June (Table 4). Of these scallops, the numbers recovered per site were highest at Croisilles (n = 128), Parapara (n = 84), Bark (n = 48), and Wainui (n = 47), and lowest at Motueka (n = 8) and Farewell (n = 4) (Table 4). Densities per site varied from 0.12 to 3.5 m^{-2} (Table 4) and were markedly lower than the overall estimated spat release mean density of 6.8 m^{-2} (Table 1); this decline over about three weeks may reflect both mortality and spat dispersal beyond our study sites. At most of the sites the densities with a visible check mark predominated, indicating that they were the released scallops.

Table 4: Number of small live scallops* < 60 mm recovered by site, per quadrat (4.8 m^2) and in total, in June 2018, and the calculated mean density (scallops m^{-2}); the number and density with shell check marks are shown in brackets and also expressed as the percentage with check marks. Number and density of larger live scallops (≥ 60 mm) are also provided. A dash indicates no quadrat sampled. GB, Golden Bay; TB, Tasman Bay. Sites are ordered top to bottom with increasing scallop density (scallops < 80 mm m^{-2} in December 2018) (see Table 5).

June 2018

Bay	Site	Scallops < 60 mm recovered per quadrat									Quadrats (*n*)	Small scallops (< 60 mm) Number recovered (scallops)	Small scallops (< 60 mm) Mean density (no. m^{-2})	Small scallops (< 60 mm) Percentage w. check mark	Larger scallops ≥ 60 mm Number recovered (scallops)	Larger scallops ≥ 60 mm Mean density (no. m^{-2})
		1	2	3	4	5	6	7	8	9						
GB	Parapara	0	28	29	27	0	–	–	–	–	5	84 (83)	3.50 (3.46)	99	0	0.00
TB	Motueka	5	3	0	0	–	–	–	–	–	4	8 (8)	0.42 (0.42)	100	0	0.00
TB	Awaroa	5	1	9	2	2	3	–	–	–	6	22 (19)	0.76 (0.66)	86	0	0.00
GB	Patons	1	0	15	3	1	3	0	0	–	8	23 (23)	0.60 (0.60)	100	0	0.00
GB	Puponga	0	0	0	1	11	13	0	0	–	8	25 (25)	0.65 (0.65)	100	0	0.00
GB	Farewell	0	0	2	1	1	0	0	–	–	7	4 (2)	0.12 (0.06)	50	1	0.03
TB	Croisilles	44	46	0	5	7	10	8	0	8	9	128 (90)	2.96 (2.08)	70	93	2.15
GB	Wainui	0	4	14	5	11	3	2	8	–	8	47 (41)	1.22 (1.07)	87	11	0.29
TB	Bark	1	5	1	0	12	10	8	9	2	9	48 (39)	1.11 (0.90)	81	15	0.35
											Totals: 64	***389 (330)***			***120***	

*Excludes 63 small live scallops < 60 mm (i.e., 20 from Puponga, 39 from Parapara, 1 from Awaroa, and 3 from Croisilles) that were attached in clumps by the byssus threads of green-lipped mussels. These 'attached' scallops are shown in the June 2018 length frequency distributions in total (Figure 11) and by site (Figure 12), but were excluded from the dataset used for estimating survival and growth because no 'attached' scallops were found during the December 2018 sampling.

Scallop length frequency and density estimates in December 2018

During the May 2018 spat release deployment at the Farewell site, the strong currents caused the vessel to drift away from the marker buoy. Although the subsequent diver sampling in June and December 2018 tried to take account of this drift, it may well have missed the deployment site in June, as the sampling appears to have underestimated the June density relative to December. An additional site (Croisilles 2) within Croisilles Harbour was also sampled to provide additional data on extant scallop beds.

The length frequency distribution of all live scallops recovered in December 2018 (including at the additional site, Croisilles 2) show a clear progression in the smaller scallop mode from 10 to 50 mm in length in June (Figure 11), to 40 to 80 mm in length in December (Figure 13). The overall length frequency distribution (Figure 13) at most of the individual site plots (original sites: Figure 14; Croisilles 2 site: Figure 15) show a break in the distribution around 75 to 80 mm. We have assumed 80 mm represents the maximum size any of the scallops observed at sizes smaller than 60 mm in June would have grown to by December. For scallops smaller than 80 mm in December 2018, scallop shell length ranged from 29 to 79 mm, and half of the scallops had a shell length between 55 and 66 mm (mean and median = 60.0 mm) (Figure 13).

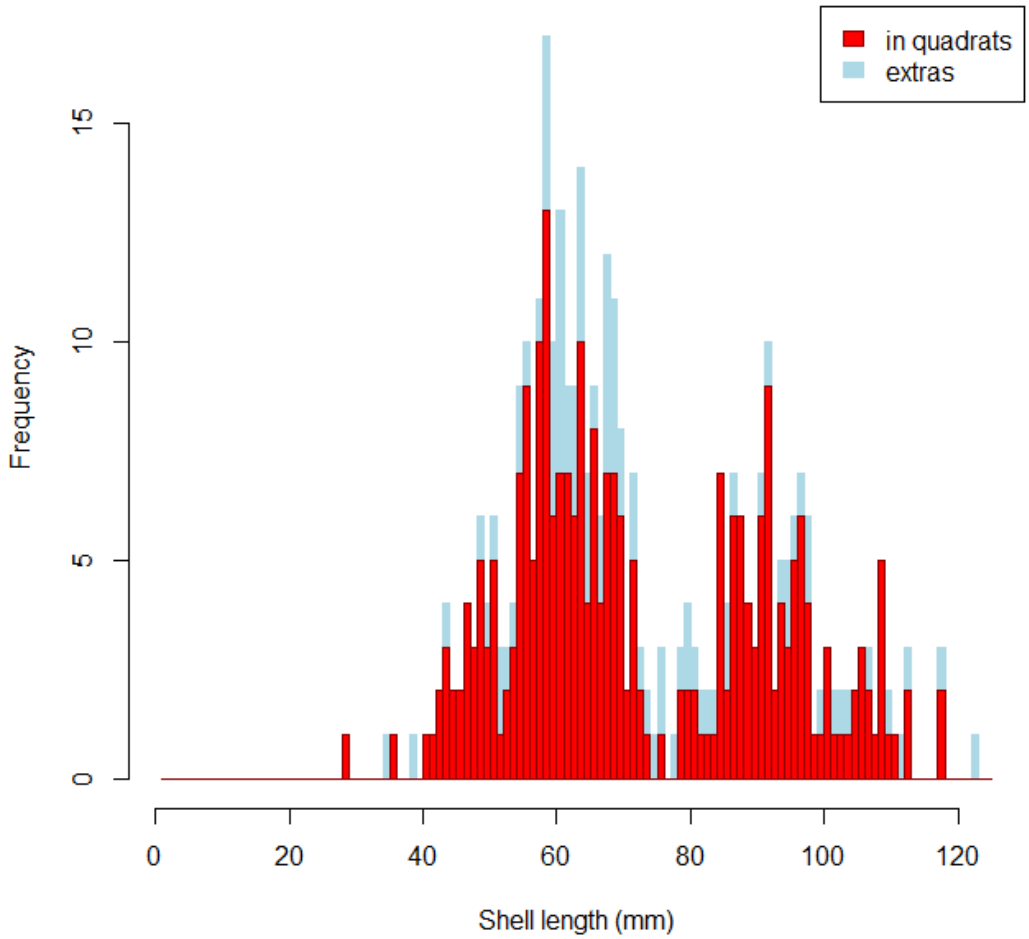

Figure 13: Length frequency distribution of live scallops collected in December 2018. Bar colour distinguishes scallops in the sampled quadrats (red) from extra scallops collected from outside the quadrats (light blue; these 'extra' scallops were collected to boost the sample size for investigating scallop condition and disease). All scallops were free-living (i.e., none were byssally attached in clumps).

Individual site length frequency distributions from December 2018 show that the most scallop individuals were recovered from Bark, Wainui, and Croisilles, with recovered scallops at Wainui and Croisilles clearly falling within the two distinct length modes (50–80 mm and 80–120 mm) (Figure 14). The same bimodal pattern was observed at Croisilles 2 (Figure 15). As in June 2018, scallops larger than 80 mm in length were only recorded at four sites: Farewell, Croisilles, Wainui, and Bark (Figure 14); this size class was also found at Croisilles 2 (Figure 15). At Parapara, Motueka, Awaroa, and Patons, only smaller (presumed released) scallops were recovered (Figure 14).

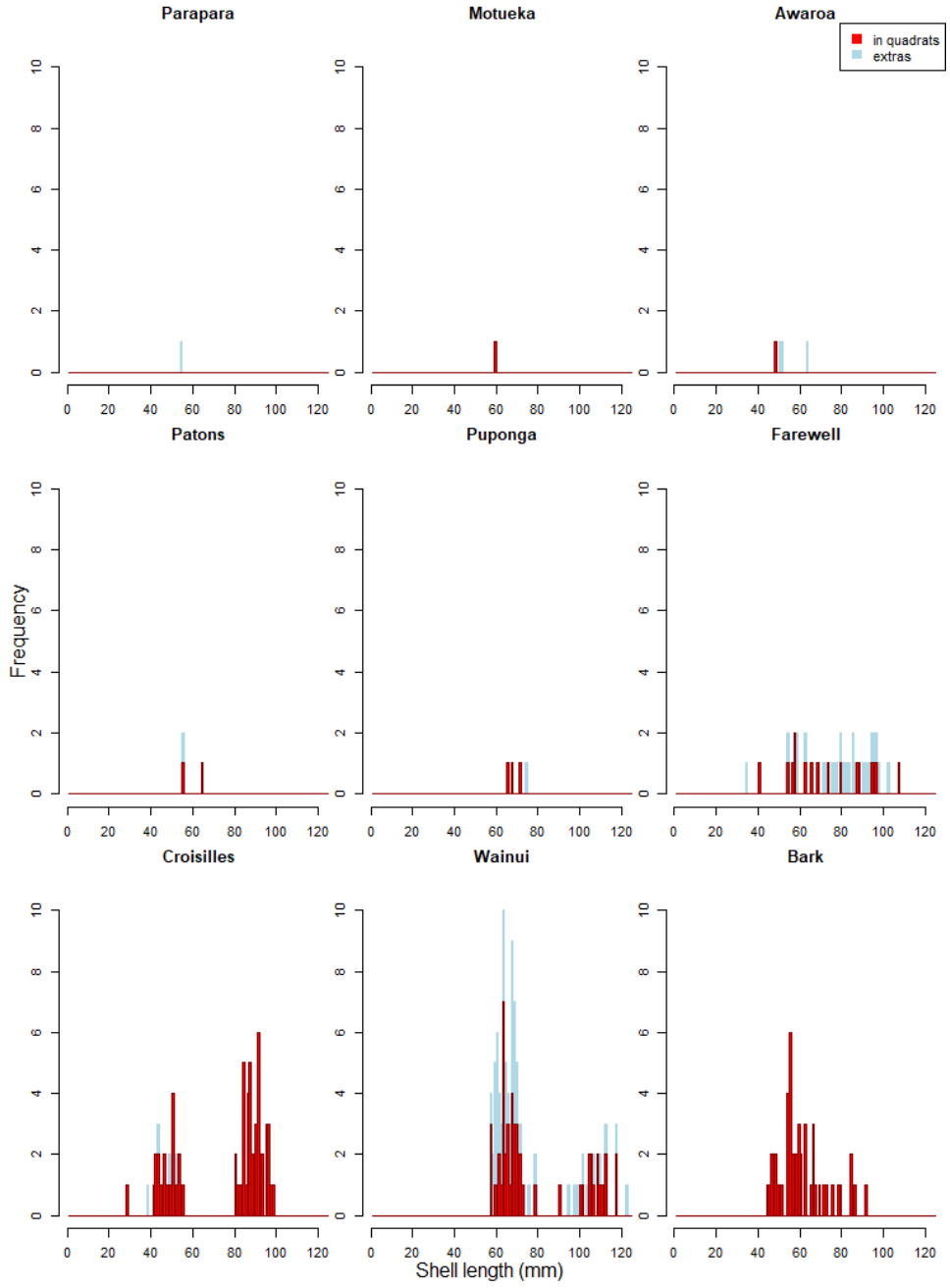

Figure 14: Length frequency distribution of live scallops collected by site in December 2018. Bar colour distinguishes scallops in the sampled quadrats (red) from extra scallops collected from outside the quadrats (light blue; these 'extra' scallops were collected to boost the sample size for investigating scallop condition and disease). All scallops were free-living (i.e., none were byssally attached in clumps). Note levels of sampling varied between sites (Table 5). Sites are ordered from top left to bottom right with increasing scallop density (scallops < 80 mm m^{-2} in December 2018) (see Table 5).

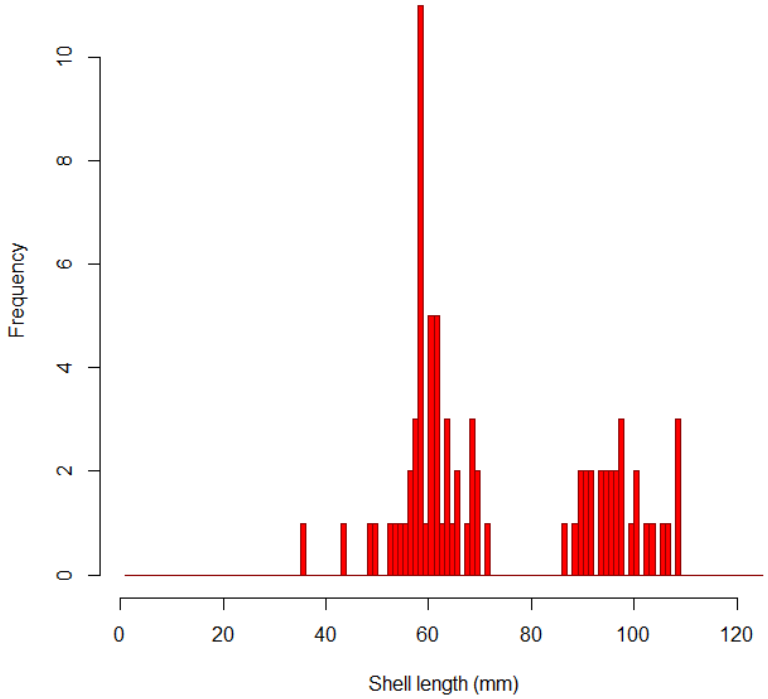

Figure 15: Length frequency distribution of live scallops collected from the Croisilles 2 site in December 2018. All scallops collected were from within the sampled quadrats (i.e., no extra scallops were collected from outside the quadrats). All scallops were free-living (i.e., none were byssally attached in clumps). This site was not enhanced or sampled in June 2018.

A total of 168 live free-living scallops smaller than 80 mm were recovered from the sampled quadrats in December 2018 (Table 5). Of these scallops, the numbers recovered per site were highest at Croisilles 2 (n = 49), Bark (n = 45), Wainui (n = 36), and Croisilles (n = 22), low at Farewell (n = 9), and minimal (n = 1–3) or nil at the other sites. Estimated densities at the sites where spat were experimentally released ranged from 0 to 0.78 m^{-2} (density was 0.85 m^{-2} at the Croisilles 2 site) and were generally lower than densities observed in June. At most of the enhanced sites the densities of spat with a visible check mark predominated, except Puponga where unchecked spat densities were slightly higher but both groups had very low densities. Check-marked spat were also recorded at Croisilles 2, a site which was not enhanced with scallop spat within this study, suggesting effects beyond enhancement may cause check marks, or possibly that the site may have received enhancement from spat releases (i.e., by industry spat-release activities) outside this study. Scallops greater than 80 mm in length were present at the same four sites that larger (greater than 60 mm) scallops were recorded in June, as well as at Croisilles 2.

Table 5: Number of small live scallops < 80 mm recovered by site, per quadrat (4.8 m^2) and in total, in December 2018, and the corresponding mean density (scallops m^{-2}); the number and density with shell check marks are shown in brackets and also expressed as the percentage with check marks. Number and density of larger scallops (≥ 80 mm) are also provided. A dash indicates no quadrat sampled, or no data available. GB, Golden Bay; TB, Tasman Bay. Sites are ordered top to bottom with increasing scallop density (scallops < 80 mm m^{-2} in December 2018).

December 2018

Bay	Site	Scallops < 80 mm recovered per quadrat												Quadrats (*n*)	Small scallops (< 80 mm) Number of recovered (scallops)	Small scallops (< 80 mm) Mean density (no. m^{-2})	Small scallops (< 80 mm) Percentage with check mark	Larger scallops (≥ 80 mm) Number of recovered (scallops)	Larger scallops (≥ 80 mm) Mean density (no. m^{-2})
		1	2	3	4	5	6	7	8	9	10	11	12						
GB	Parapara	0	0	0	0	0	0	0	0	–	–	–	–	8	0 (0)	0.00 (0.00)	–	0	0.00
TB	Motueka	0	0	0	0	0	0	1	0	–	–	–	–	8	1 (1)	0.03 (0.03)	100	0	0.00
TB	Awaroa	0	1	0	0	0	0	–	–	–	–	–	–	6	1 (1)	0.03 (0.03)	100	0	0.00
GB	Patons	0	0	0	0	0	1	0	1	–	–	–	–	8	2 (2)	0.05 (0.05)	100	0	0.00
GB	Puponga	0	0	0	0	0	2	1	0	–	–	–	–	8	3 (1)	0.08 (0.03)	33	0	0.00
GB	Farewell	2	1	0	0	2	0	0	1	3	–	–	–	9	9 (9)	0.21 (0.21)	100	6	0.14
TB	Croisilles	3	2	4	3	1	0	4	0	0	2	3	0	12	22 (18)	0.38 (0.31)	82	44	0.76
GB	Wainui	2	2	3	5	4	1	2	3	2	4	4	4	12	36 (32)	0.62 (0.56)	89	16	0.28
TB	Bark	5	4	7	5	2	3	2	8	3	5	1	0	12	45 (43)	0.78 (0.75)	96	6	0.10
TB	Croisilles 2	7	5	3	4	1	3	6	5	4	7	3	1	12	49 (16)	0.85 (0.28)	33	29	0.50
														Totals: 95	***168 (123)***			***101***	

Scallop survival and growth estimates

Numbers of scallops recovered by length bin at each site for each sampling event are presented in Figure 16, with numbers at length converted into densities (scallops m^{-2}) in Figure 17. Mean density and median length by cohort at each site for each sampling event are summarised in Table 6 and Table 7, respectively. When the numbers of scallops (Figure 16) and scallop density (scallops m^{-2}, Figure 17) recovered by length bin at each site in June and December 2018 are visualised and compared, the decline in abundance and growth progression of the smaller (putative 2018) cohort can clearly be seen at most sites. At the Farewell site, the numbers of scallops recovered on both sampling occasions were low (Table 6). This suggests that the enhanced location at this site was not well sampled; therefore results based on the sampling at Farewell (density in June and December, survival between June and December) may not accurately reflect the conditions at this site.

Survival estimates for the 2018 cohort during the study period (Table 6) were calculated using the estimated spat release densities in May (for the May–June and May–December estimates) and the diver-sampled scallop densities in June and December (for the June–December estimates). Initial survival of the 2018 cohort between the time of spat release at the end of May and the diver sampling three weeks later in June was ~50% at Parapara and Croisilles, ~20% at Wainui and Bark, and only ~10% or lower at the other sites. Survival of the remaining 2018 cohort between June and December was relatively high at Bark (70%) and Wainui (51%), low at Croisilles (13%), Puponga (12%), and Patons (9%), minimal at Motueka (6%) and Awaroa (5%), and nil at Parapara (0%). The June–December estimate of survival at Farewell was implausibly high (175%) suggesting that the site was not well sampled. Overall survival of the 2018 cohort between May and December was highest at Bark (12%) and Wainui (10%), intermediate at Croisilles (6%) and Farewell (3%, noting this estimate is less reliable), and minimal (1% or less) at the other sites.

Using the diver-sampled scallop density data from the June to December period, mortality rates were derived and expressed as annual proportional mortality (A) and instantaneous mortality (M), to enable comparison with estimates from previous studies: predicted mortality rates were relatively high at Bark (A = 51% M = 0.70) and Wainui (A = 74% M = 1.34), and extremely high at all other sites (A = ≥ 98%, M = > 4.0) (Table 6).

Based on the median shell length of the overall scallop population sampled across all sites in May (21 mm; Figure 10), June (27 mm, for scallops smaller than 60 mm; Figure 11), and December 2018 (60 mm, for scallops smaller than 80 mm; Figure 13), scallop growth increments were 6 mm between May and June, 33 mm between June and December and 39 mm between May and December 2018. These absolute growth increments can also be expressed as relative growth increments (i.e., the proportional increase in median shell length between two time points, relative to the median shell length at the initial time point): 0.29 between May and June, 1.22 between June and December, and 1.86 between May and December 2018.

Relative growth increments by site are presented in Table 7. The greatest relative growth increment over the May to December period (assuming a median size of 21 mm in May, from released spat) was at the Puponga site (2.33) but was based on only three scallops recovered from the quadrats sampled in December. Wainui, Farewell, and Bark (with December recoveries of n = 36, 9, and 45 scallops, respectively) had intermediate relative growth increments of 2.10, 1.81, and 1.71, respectively. Motueka and Patons also had intermediate growth (1.86 and 1.71, respectively) and Awaroa had lower growth (1.43) but the calculated increments are based on minimal recoveries in December (only n = 1–2 individuals). Growth at Croisilles (n =22 individuals recovered in December) was lowest (1.33). No scallops were recovered from inside the sampled quadrats at Parapara in December; instead, the shell length (49 mm) of the single ‘extra’ scallop found outside the sampled quadrats was used as the median length for December, resulting in a relative growth increment of 1.33 at Parapara.

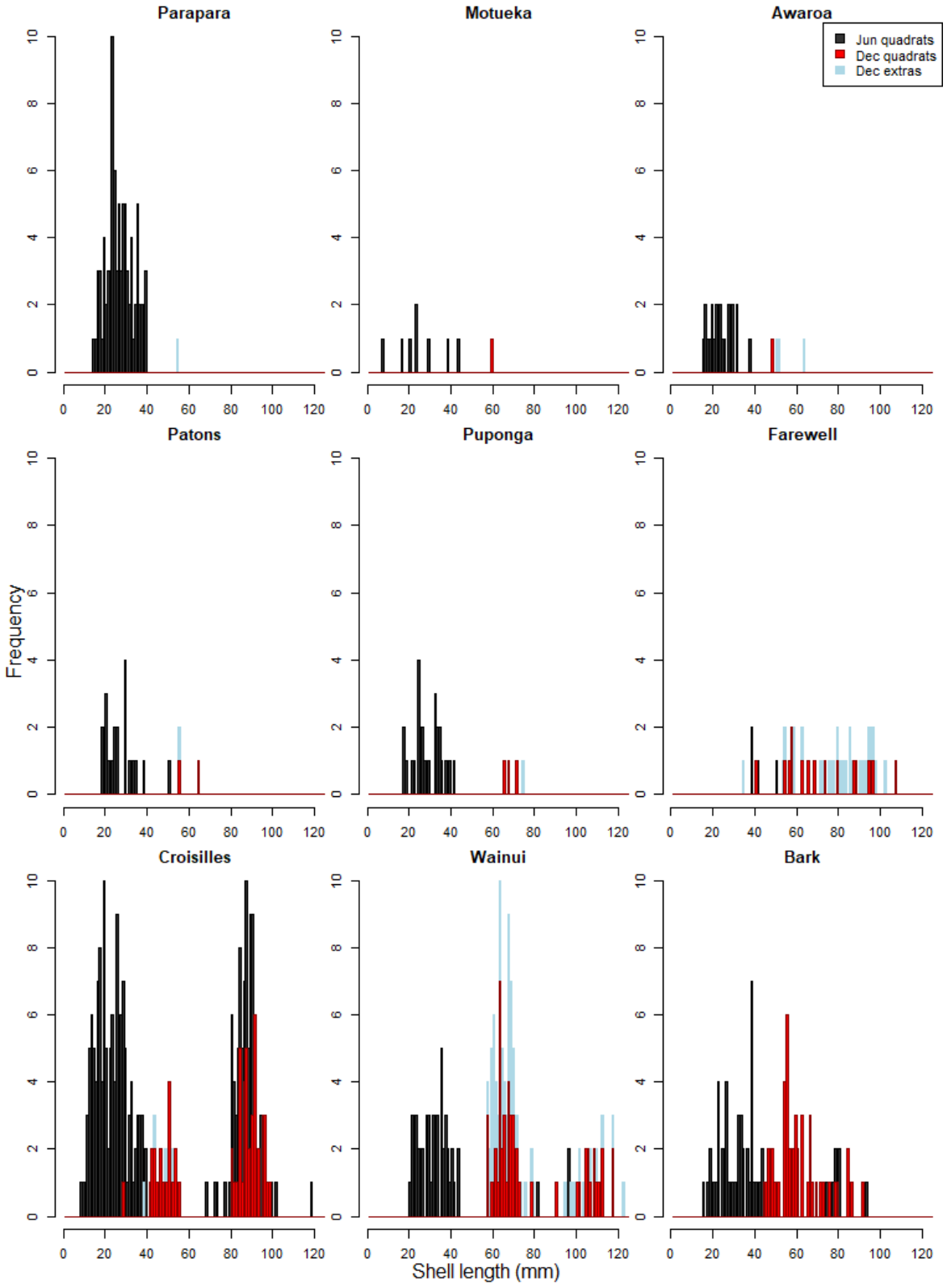

Figure 16: Length frequency distribution of live scallops recovered at each site in June (black) and December 2018 (red denotes scallops in quadrats; light blue denotes 'extra' scallops collected outside the quadrats). All scallops were free-living. Note levels of sampling varied between sites in June (64 quadrats in total; Table 4) and December (83 quadrats in total; Table 5). Sites are ordered from top left to bottom right with increasing scallop density (scallops < 80 mm m^{-2} in December 2018) (see Table 5).

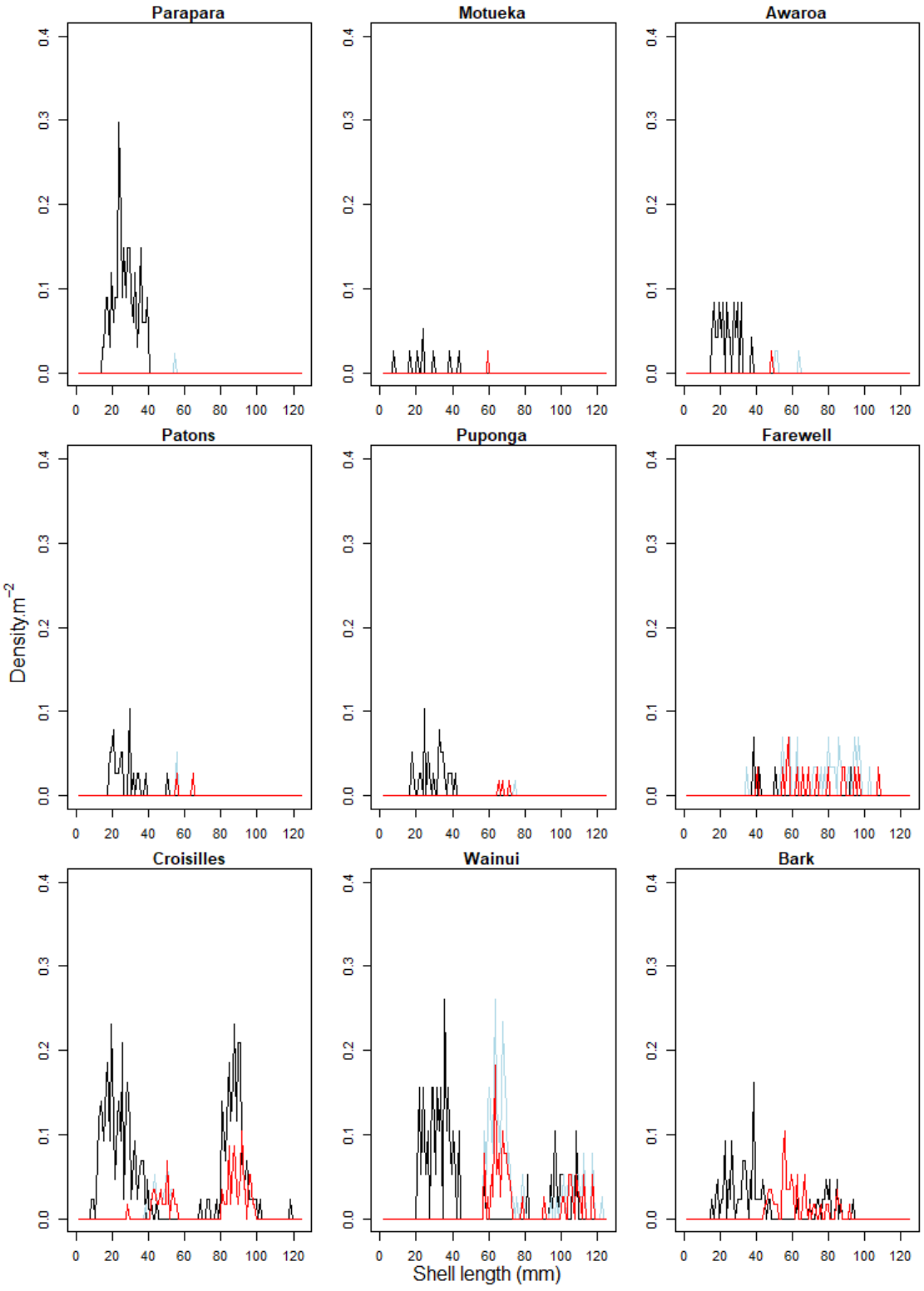

Figure 17: Live scallop density (scallops m^{-2}) at length by site in June (black) and December 2018 (red denotes scallops in quadrats; light blue denotes 'extra' scallops collected outside the quadrats). All scallops were free-living. Note levels of sampling varied between sites in June (64 quadrats in total; Table 4) and December (83 quadrats in total; Table 5). Sites are ordered from top left to bottom right with increasing scallop density (scallops < 80 mm m^{-2} in December 2018) (see Table 5).

Table 6: Number of live free-living scallops recovered from within quadrats (each 4.8 m^2) and mean density (scallops m^{-2}) by sampling event, and estimated relative survival (density$_2$/density$_1$), for small scallops in the putative 2018 cohort and for larger scallops. Bays: GB, Golden Bay; TB, Tasman Bay. Months: M, May; J, June, D, December 2018. Mean density for May was calculated from the estimated number of spat released within the deployment area at each site (see Table 1). A dash indicates no data available. Sites are ordered top to bottom with increasing scallop density (scallops < 80 mm m^{-2} in December 2018) (see Table 5). Using the data from the June to December period, derived mortality rates are also presented, as annual proportional mortality (*A*) and instantaneous mortality (*M*), for comparison with estimates from previous studies. Mortality rates for Parapara and Farewell were not calculated due to data limitations for those sites.

				Small scallops (2018 cohort: < 60 mm in May/Jun, < 80 mm in Dec)										Larger scallops				
Bay	Site	Quadrats (*n*)		Scallops (*n*)		Density (m^{-2})			Survival (proportion)			Derived mortality rates: Annual proportional (*A*) and instantaneous (*M*)		Scallops (*n*)		Density (m^{-2})		Survival (prop)
		J	D	J	D	M	J	D	M–J	J–D	M–D	*A*	*M*	J	D	J	D	J–D
GB	Parapara	5	8	84	0	7.27	3.50	0	0.48	0	0	1.00	–	0	0	0	0	–
TB	Motueka	4	8	8	1	6.50	0.42	0.03	0.06	0.06	<0.01	> 0.99	5.55	0	0	0	0	–
TB	Awaroa	6	6	22	1	7.01	0.76	0.03	0.11	0.05	<0.01	> 0.99	6.18	0	0	0	0	–
GB	Patons	8	8	23	2	6.63	0.60	0.05	0.09	0.09	0.01	> 0.99	4.88	0	0	0	0	–
GB	Puponga	8	8	25	3	7.14	0.65	0.08	0.09	0.12	0.01	0.99	4.24	0	0	0	0	–
GB	Farewell	7	9	4	9	6.50	0.12	0.21	0.02	1.75	0.03	–	–	1	6	0.03	0.14	4.67
TB	Croisilles	9	12	128	22	6.50	2.96	0.38	0.46	0.13	0.06	0.98	4.10	93	44	2.15	0.76	0.35
GB	Wainui	8	12	47	36	6.38	1.22	0.63	0.19	0.51	0.10	0.74	1.34	11	16	0.29	0.28	0.97
TB	Bark	9	12	48	45	6.38	1.11	0.78	0.17	0.70	0.12	0.51	0.70	15	6	0.35	0.10	0.30
TB	Croisilles 2	–	12	–	49	–	–	0.85	–	–	–	–	–	–	29	–	0.50	–
	Totals	***64***	***95***	***389***	***168***									***120***	***101***			

Table 7: Median shell length of live scallop spat on release (May) and of live free-living scallops recovered from within quadrats (each 4.8 m^2) by sampling event, and estimated absolute ($length_2$-$length_1$) and relative ([$length_2$-$length_1$]/$length_1$) growth increments, for small scallops in the putative 2018 cohort and for larger scallops. Bays: GB, Golden Bay; TB, Tasman Bay. Months: M, May; J, June, D, December 2018. A dash indicates no data available. Sites are ordered top to bottom with increasing scallop density (scallops < 80 mm m^{-2} in December 2018) (see Table 5).

		Small scallops (2018 cohort: < 60 mm in May/June, < 80 mm in December)										Larger scallops					
		Scallops (*n*)		Length (mm)			Absolute increment (mm)			Relative increment (prop.)			Scallops (*n*)		Length (mm)		Abs. incr.	Rel. incr.
Bay	Site	J	D	M	J	D	M–J	J–D	M–D	M–J	J–D	M–D	J	D	J	D	J–D	J–D
GB	Parapara	84	0	21	27	*49	6	*22	*28	0.29	*0.81	*1.33	0	0	–	–		–
TB	Motueka	8	1	21	24	60	3	36	39	0.14	1.50	1.86	0	0	–	–		–
TB	Awaroa	22	1	21	24	51	3	27	30	0.14	1.13	1.43	0	0	–	–		–
GB	Patons	23	2	21	25	57	4	32	36	0.19	1.28	1.71	0	0	–	–		–
GB	Puponga	25	3	21	30	70	9	40	49	0.43	1.33	2.33	0	0	–	–		–
GB	Farewell	4	9	21	41	59	20	18	38	0.95	0.44	1.81	1	6	93	90	3	-0.03
TB	Croisilles	128	22	21	23	49	2	26	28	0.10	1.13	1.33	93	44	88	89	1	0.01
GB	Wainui	47	36	21	33	65	12	32	44	0.57	0.97	2.10	11	16	100	107	7	0.07
TB	Bark	48	45	21	33	57	12	24	36	0.57	0.73	1.71	15	6	79	86	7	0.09
TB	Croisilles 2	–	49	–	–	60	–	–	–	–	–	–	–	29	–	97		–
	Totals	***389***	***168***										***120***	***101***				

* No scallops were recovered from inside the sampled quadrats at Parapara in December; instead, the shell length (49 mm) of the single 'extra' scallop found outside the sampled quadrats at Parapara was used as the median length for December, and for calculating the Jun–Dec and May–Dec growth increments for this site.

Scallop condition in December 2018

Scallop tissue weight (from December 2018 samples) increased with scallop length (Figure 18, top), however examination of residuals by site did not reveal any clear differences in scallop condition among sites (Figure 18, bottom).

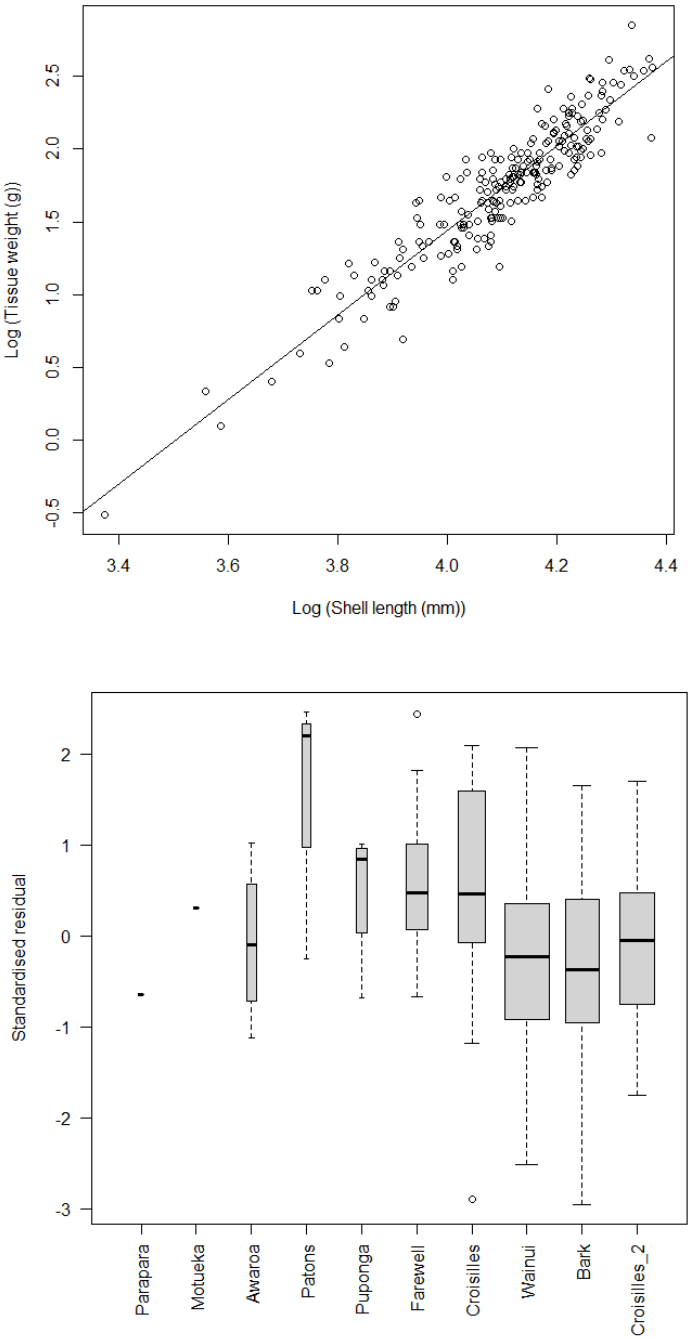

Figure 18: Relationship between scallop tissue weight (wet weight, g) and shell length (mm) in scallops < 80 mm collected in December 2018 (*n* = 229 scallops in total, comprising 166 scallops from the sampled quadrats plus 63 extra scallops found outside the quadrats while swimming along the transects, collected to increase the sample size for investigating condition). Top: Tissue weight increased significantly with length: Log (tissue weight) ~ -10.161 + 2.901 * log (length); p <0.0001, R^2 = 0.866). Bottom: Boxplot of scallop condition standardised residuals by site. Sites are ordered from left to right with increasing scallop density (scallops < 80 mm m^{-2} in December 2018) (see Table 5). Results were similar when the 'extra' scallops collected were excluded.

4.2 Environmental characteristics

Depth, current speed, and sea surface water clarity

The depth range sampled across the sites was 6 to 17 m (Table 8; depths corrected to Lowest Astronomical Tide). Most sites were between 12 and 17 m, but the Wainui and Bark sites were shallower at 6 and 8 m, respectively. Maximum current speeds (95th percentile of current flow measured with ADCP) were lowest at Parapara (0.100 m s^{-1}) and highest at Farewell (0.275 m s^{-1}) (Table 8). Water clarity, measured vertically from the sea surface using Secchi disc readings, was lowest at Motueka (3.3 m) and highest at Farewell (13.0 m) (Table 8). There was no apparent relationship between scallop density and either depth, maximum current speed, or water clarity (Table 8).

Table 8: Site depths, current speeds, and water clarities. Depths corrected to Lowest Astronomical Tide. A dash indicates no data available. GB, Golden Bay; TB, Tasman Bay. Sites are ordered top to bottom with increasing scallop density (scallops < 80 mm m^{-2} in December 2018) (see Table 5).

Bay	Site	Density (scallops m^{-2})	Depth (m)	Current speed 95th percentile (m s^{-1})	Water clarity, measured using secchi disc (m)
GB	Parapara	0	15.1	0.100	4.9
TB	Motueka	0.03	14.5	0.134	3.3
TB	Awaroa	0.03	17.0	0.138	6.8
GB	Patons	0.05	14.6	0.154	4.5
GB	Puponga	0.08	16.5	0.204	4.0
GB	Farewell	0.21	17.0	0.275	13.0
TB	Croisilles	0.38	13.3	0.144	7.7
GB	Wainui	0.62	6.0	0.135	4.1
TB	Bark	0.78	7.5	0.154	4.6
TB	Croisilles 2	0.85	12.5	–	7.4

Sediment properties

Sediment samples were collected at each site in June and December 2018 except at Croisilles 2 which was only sampled in December. Sediment data at each site appeared consistent between the June and December sampling time points, so data from all samples/times from a site were pooled to examine collinearity using a pairs plot (Figure 19).

Across all samples, multiple sediment variables were correlated (Figure 19). The % silt content and % clay content were strongly positively correlated with each other (correlation coefficient = 0.9); both were strongly negatively correlated with % coarse sand, % medium sand, and % fine sand (correlations = −0.9 to −0.7), and % silt was moderately negatively correlated with % very fine sand (correlation = −0.5). Consequently, % mud content was calculated (% mud = % silt + % clay) and used as a key sediment grain size variable in our data analysis.

As can be expected, % mud was strongly negatively correlated with % fine sand, % medium sand, and % coarse sand (correlations = −1.0 to −0.7), and moderately negatively correlated with % very fine sand (correlation = −0.4); % mud was also strongly negatively correlated with sediment compressibility (correlation = −0.7) and strongly positively correlated with sediment softness and % organic content (correlations = 0.8) (Figure 19).

Sediment chlorophyll *a*, an indicator of the presence of fresh microalgal food (settled phytoplankton and microphytobenthos), was moderately positively correlated with % fine sand, % coarse sand, and sediment compressibility (correlations = 0.4 to 0.5), and moderately negatively correlated with % mud (correlation = −0.4) (Figure 19). Sediment chlorophyll *a* was moderately positively correlated with

phaeopigment (correlation = 0.4). Phaeopigment is a non-photosynthetic degradation product of algal chlorophyll *a* pigments. Phaeopigment was moderately positively correlated with sediment softness and % organic matter content (correlations = 0.4 and 0.5, respectively).

Depth was moderately positively correlated with % mud, sediment softness, and % organic content (correlations = 0.5) and strongly negatively correlated with % coarse sand (correlation = −0.7). Current speed was strongly positively correlated with % medium sand (correlation = 0.8) and moderately negatively correlated with % mud (correlation = -0.6).

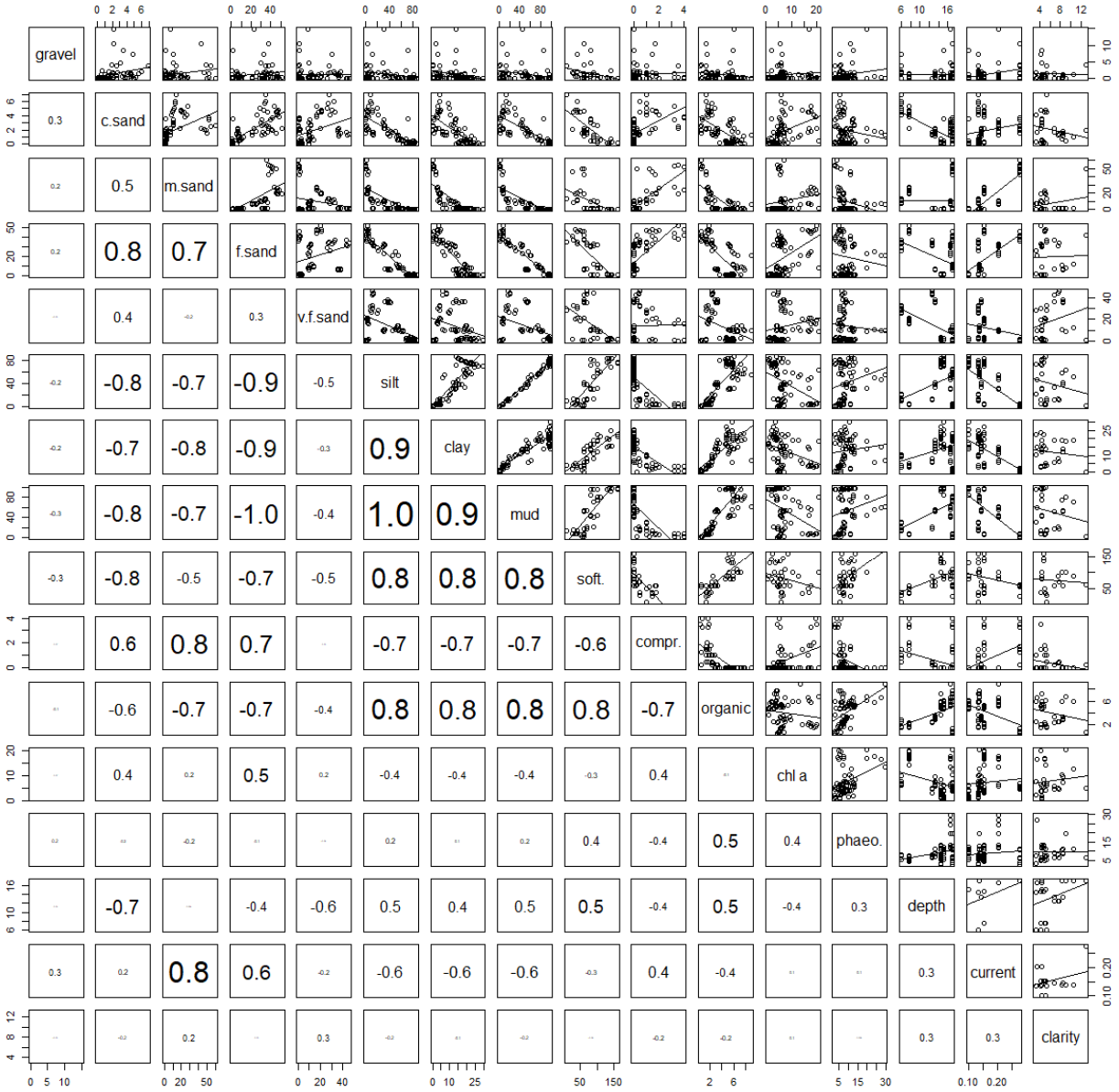

Figure 19: Pairs plot (scatterplots on upper right, correlation coefficients on lower left) showing the relationships between the different sediment variables (percentage content of the different grain size categories of gravel, coarse sand, medium sand, fine sand, very fine sand, silt, clay, and mud (i.e., silt + clay); sediment softness and compressibility; percentage content of organic matter; sediment chlorophyll *a* and phaeopigment concentrations) and the environmental site variables of water depth, maximum (95th percentile of) current speed, and water clarity (measured using Secchi disc readings). Font size indicates the strength of the correlation coefficients.

Examination of the average grain size composition across all samples and sampling times per site (Table 9), shows a strong positive relationship between scallop density (scallops < 80 mm in December) and the percentage of fine and very fine sand (i.e., fine sand + very fine sand) content in the sediment, with the highest densities of scallops present at sites with sediment of fine and very fine sand content of 41–77% (Table 9). Conversely, as can be expected given the strong correlation between fine sands and mud, there was a strong negative relationship between scallop density and the percentage of mud (i.e., silt + clay) in the sediment; the lowest densities of scallops were observed at the sites with sediment mud content of 95–97% (Table 9).

Table 9: Sediment grain size composition (%) by site (mean values, calculated using all replicate samples from June and December 2018). Grain size categories: G, gravel/shell hash (>2000 µm); CS, coarse sand (500–2000 µm); MS, medium sand (250–500 µm); FS, fine sand (125–250 µm); VFS, very fine sand (62.5–125 µm); silt (3.9–62.5 µm); and clay (< 3.9 µm). The three columns on the right show the same sand, silt, and clay data summed into two categories of sand and one category of mud. Sites are ordered top to bottom with increasing scallop density (scallops < 80 mm m^{-2} in December 2018) (see Table 5).

	Density	Gravel				Sand		Mud		Sand	Mud
Site	(scallops m^{-2})	G	CS	MS	FS	VFS	Silt	Clay	CS+ MS	FS+ VFS	Silt+ Clay
Parapara	0	1	1	0	1	1	77	19	1	2	96
Motueka	0.03	0	0	0	1	3	74	21	1	4	95
Awaroa	0.03	0	1	2	9	11	57	20	2	20	77
Patons	0.05	0	0	0	0	2	76	21	0	3	97
Puponga	0.08	3	2	9	27	10	38	11	11	37	49
Farewell	0.21	3	3	51	40	1	2	1	54	41	3
Croisilles	0.38	1	2	1	6	36	38	15	3	43	53
Wainui	0.62	3	5	11	32	29	13	6	16	62	20
Bark	0.78	1	4	22	47	19	4	4	27	66	7
Croisilles 2	0.85	0	1	2	33	44	12	7	4	77	19

Boxplots of sediment variables by site provide further insight into patterns between sediment properties and scallop density (Figure 20; sites are ordered left to right with increasing scallop density (scallops < 80 mm in December 2018)). These confirmed the observed patterns of increasing scallop density with increasing sandiness and decreasing muddiness of the sediments. Sites with the lowest scallop densities, Parapara, Motueka, Awaroa, and Patons, had sediments with greater than 75% mud (silt + clay), while Croisilles and Puponga had 40–50% sediment mud content. In general, sites with sandier sediments, containing less than 20% mud content (Farewell, Wainui, Bark, and Croisilles 2), had a higher density of scallops.

The boxplots in Figure 20 also show sediment softness, compressibility, organic matter content, and chlorophyll *a* and phaeophytin concentrations. The muddier sediment sites with lower scallop density (Parapara, Motueka, Awaroa, Patons, and Puponga) were substantially softer, had minimal compressive strength, and had a higher organic content (5–7% g^{-1} sediment) compared with the sandier sediment sites (Farewell, Croisilles, Wainui, Bark, and Croisilles 2). This can be expected as sediment mud content was highly positively correlated with sediment softness and organic content (correlation coefficients = 0.8; Figure 19) and highly negatively correlated with sediment compressibility (correlation = −0.7). In general, sediment chlorophyll *a* concentration increased with increasing scallop density, although Croisilles 2 sediment had a low chlorophyll *a* concentration and the highest scallop density in December 2018. Bark Bay had the highest sediment chlorophyll *a* concentration in the range from 13 to 20 µg g^{-1} sediment. No relationship was apparent between sediment phaeopigment and scallop density: phaeophytin levels were variable among sites, and only Puponga exhibited markedly higher levels than the other sites, ranging from 12 to 30 µg g^{-1} sediment.

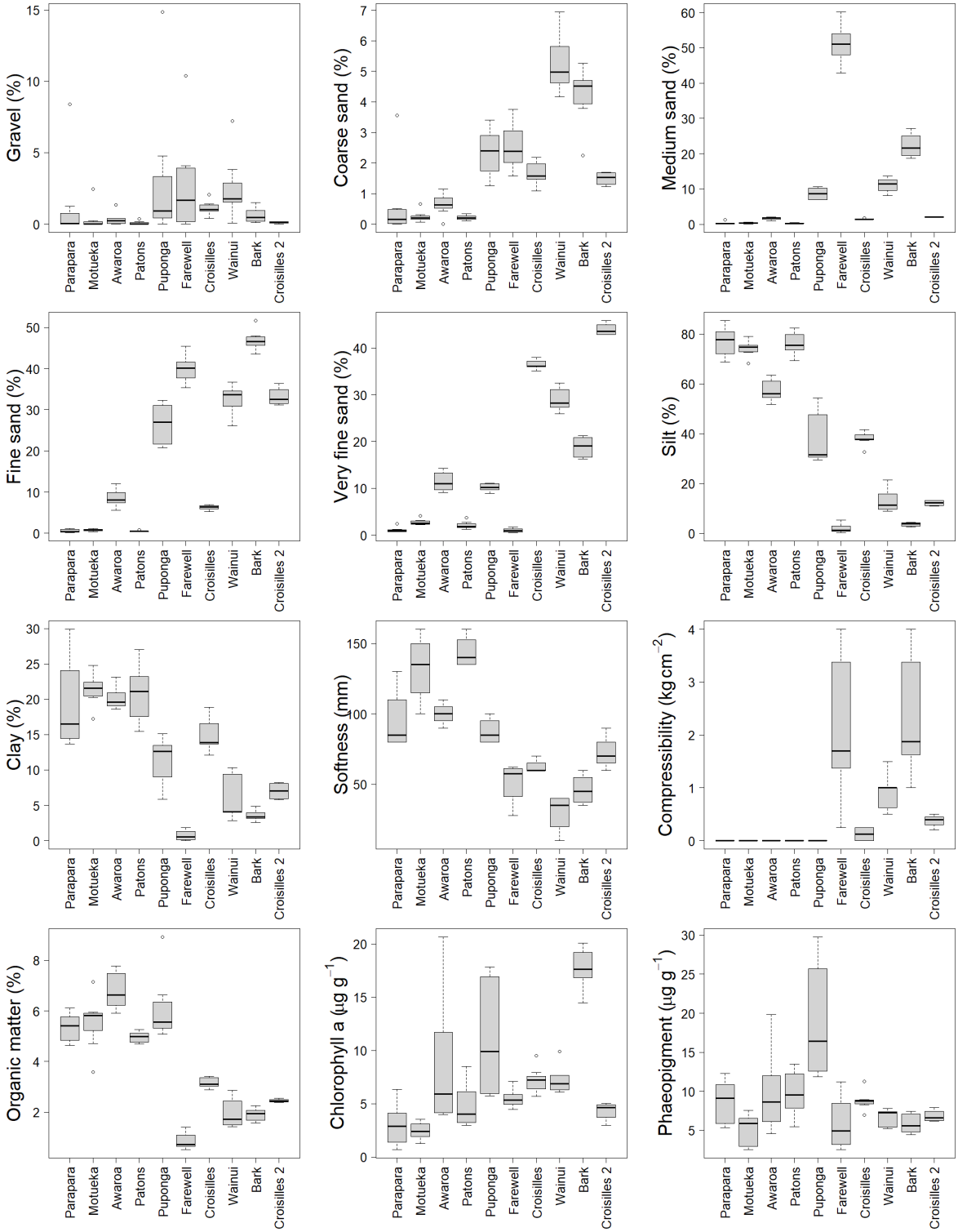

Figure 20: Boxplots of sediment variables by site, measured from seabed surface scrape samples (percentage gravel, coarse sand, medium sand, fine sand, very fine sand, silt, and clay content; percentage organic matter content; and chlorophyll *a* and phaeopigment concentrations (µg g^{-1} sediment)) and sediment measurements (sediment softness, the vertical penetration depth in mm measured using a 1-kg weighted steel ruler; sediment compressibility, the compressive strength in kg cm^{-2} measured using a handheld soil penetrometer with attached 36 mm diameter foot (values are as measured, without correction applied for the use of the attached foot). Sites are ordered left to right with increasing scallop density (scallops < 80 mm in December 2018).

Seawater properties

Seawater sample data from all samples/times from a site were pooled to examine collinearity using a pairs plot (Figure 21). Several seawater variables were highly positively correlated with each other (correlation coefficients of 0.9 to 1.0: between suspended solids, volatile suspended solids, and inorganic suspended solids; and between particulate carbon, particulate nitrogen, and turbidity) (Figure 21), so a subset of the seawater variables (dissolved oxygen, chlorophyll *a*, suspended solids, particulate carbon) was examined for any between site differences.

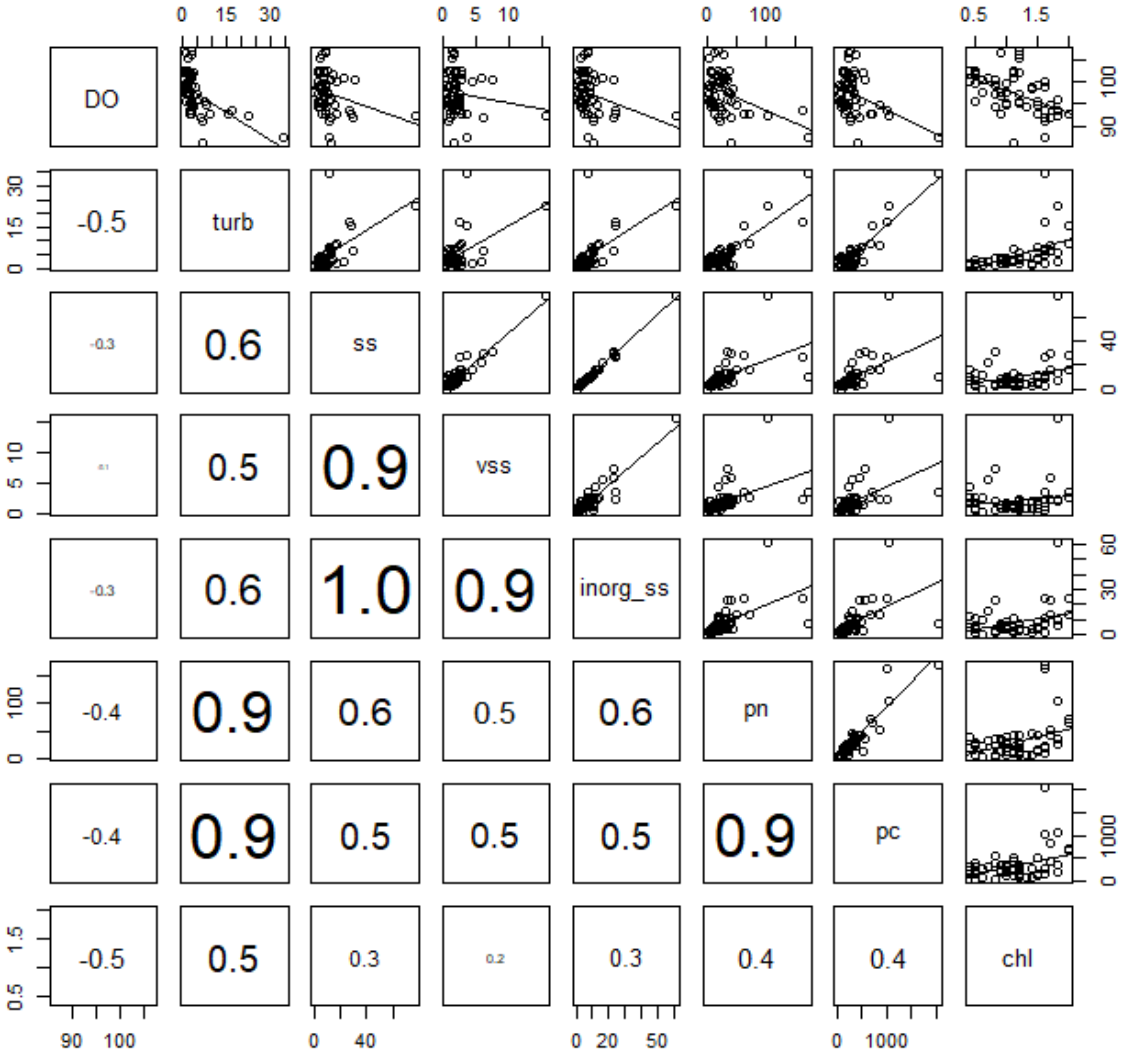

Figure 21: Pairs plot (scatterplots on upper right, correlation coefficients on lower left) of all data (combined samples collected at 0, 1, and 5 m above the seabed) for water parameters. DO =dissolved oxygen, turb = turbidity, ss = suspended solids, vss = volatile suspended solids, inorg_ss = inorganic suspended solids, pn = particulate nitrogen, pc = particulate carbon, chl =chlorophyll *a*. Font size indicates the strength of the correlation coefficients.

Boxplots of the subset of seawater covariates by site (Figure 22) showed a pattern of increasing dissolved oxygen levels with increasing scallop density, although the oxygen levels measured were all high (median values greater than 90%). A pattern of decreasing seawater chlorophyll *a* concentration with increasing scallop density was also suggested, with the highest scallop densities observed at the lowest chlorophyll *a* levels, and vice versa (cf. Croisilles 2 and Parapara; Figure 22). The other examined seawater factors of suspended solids and particulate carbon were relatively similar across all sites with no obvious patterns in relation to scallop density (Figure 22).

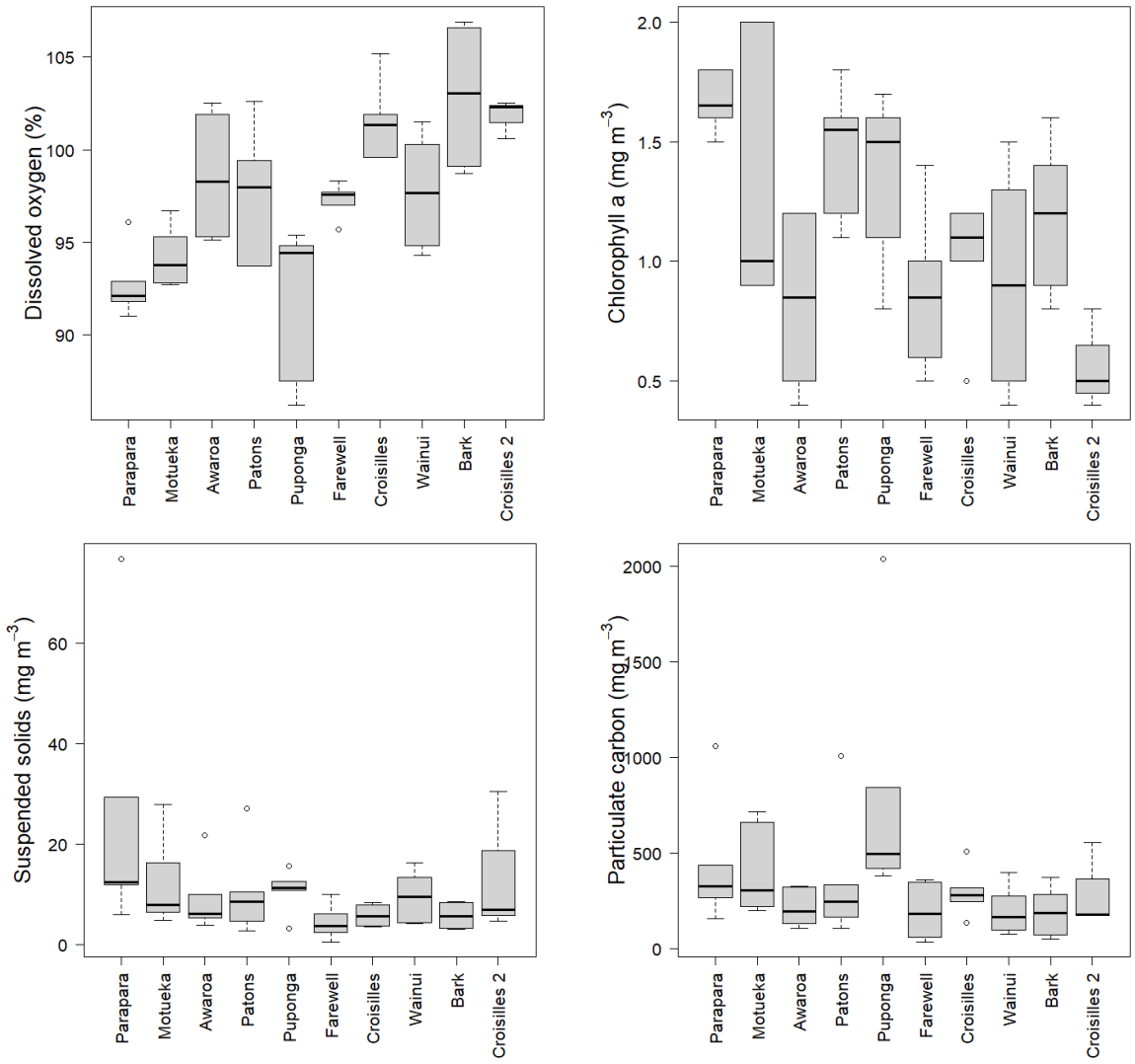

Figure 22: Boxplots of seawater variables by site, measured from seawater bottle samples collected by divers: dissolved oxygen (%, top left); total suspended solids (g m^{-3}, bottom left); chlorophyll *a* (mg m^{-3}, top right); and particulate carbon (mg m^{-3}, bottom right). Sites are ordered left to right with increasing scallop density (scallops < 80 mm in December 2018).

A Principal Component Analysis (PCA) of the average seawater and sediment environmental parameters explained 73% of the variation with the first two principal components (Figure 23) and 96% with five components. Over 52% of the variation was accounted for by the first principal component, which separated most of the sites in relation to % mud and % organic content in the sediment, suspended solids and chlorophyll *a* in the seawater (-ve eigenvector on PC1), and dissolved oxygen in the seawater (+ve eigenvector on PC1) (Figure 23). The Puponga site was separated from this main gradient of conditions by the second principal coordinate, related to +ve eigenvector coefficients for phaeopigment and chlorophyll *a* concentrations in the sediment and particulate carbon in the seawater (Figure 23).

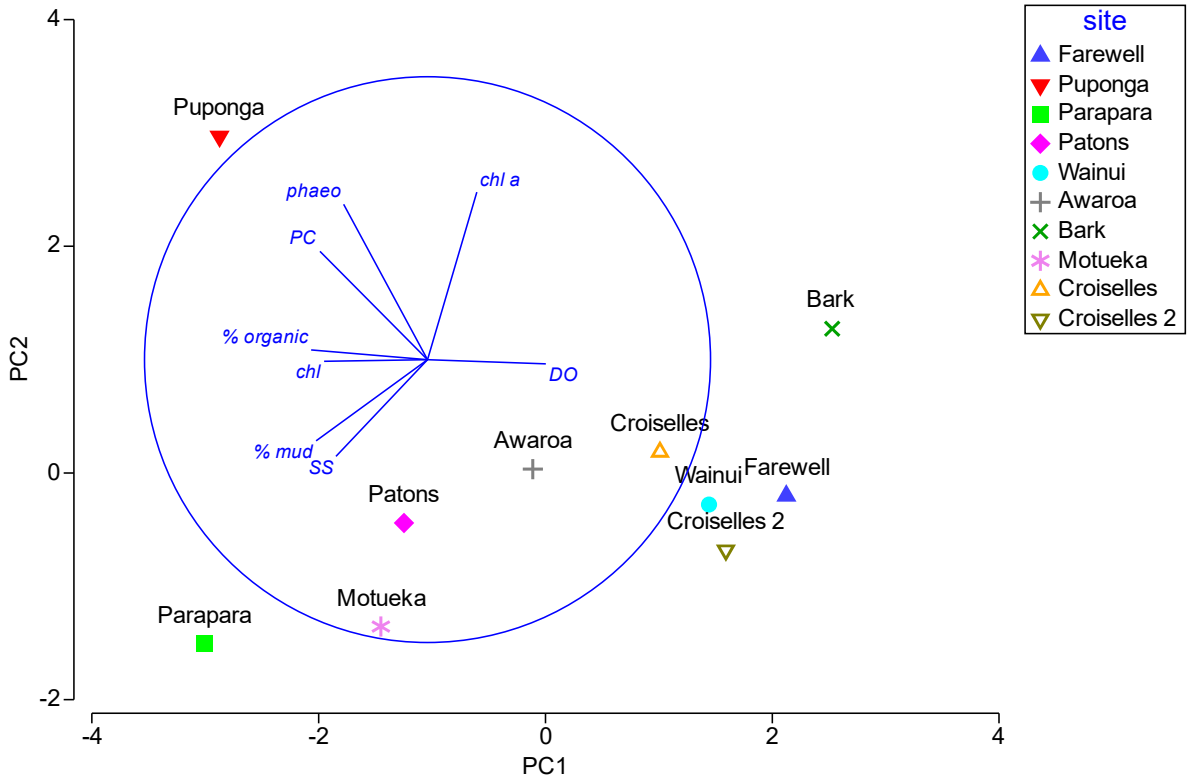

Figure 23: Study sites and environmental drivers along the first two axes of the Principal Components Analysis. Sites with more similar characteristics are positioned closer together on the plot. The length of the line in the overlay plot (blue) represents the importance of that environmental variable in explaining differences between sites. Variables shown are the percentage composition of mud and organic content in the sediments (% mud and % organic), chlorophyll *a* in the sediments (chl a), and concentrations of suspended solids (SS), dissolved oxygen (DO), chlorophyll *a* (chl), phaeophytin (phaeo), and particulate nitrogen in the seawater.

4.3 Ecological characteristics

Benthic macrofauna

Benthic macrofaunal communities were typical of soft sediment sandy mud communities, dominated by the polychaete worms *Owenia petersenae* (Oweniidae tubeworm) and *Barantolla lepte* (Capitellidae), and the bivalve *Theora lubrica* in June 2018, and in December 2018 by *O. petersenae* and *B. lepte*, and the polychaete tubeworm *Spiochaetopterus* sp. There were some June to December differences in community composition as would be expected with sampling in different seasons, but the samples from individual sites were generally clustered in the same area of the ordination space (Figure 24). Within this pattern, samples from the original Croisilles site were quite variable in December.

In general, the muddier sites with a higher organic content are clustered together (e.g., Motueka, Patons, Parapara) with the less muddy (i.e., sandier) sites in a separate cluster (Farewell, Wainui, Bark, and Croisilles 2). Motueka, Patons, and Parapara were dominated by *Theora lubrica* (Semelidae bivalve), *Aglaophamus macroura* (Nephtyidae worm), Cirratulidae worm (identification to family only), and *Cossura consimilis* (Cossuridae worm). Farewell, Wainui, Bark, and Croisilles 2 were dominated by *Barantolla lepte*, *Owenia petersenae*, *Pseudopolydora paucibranchiata* (Spionidae worm), and *Torridoharpinia hurleyi* (Phoxocephalid amphipod). The Croisilles and Awaroa sites had within site similarity dominated by species from both groups.

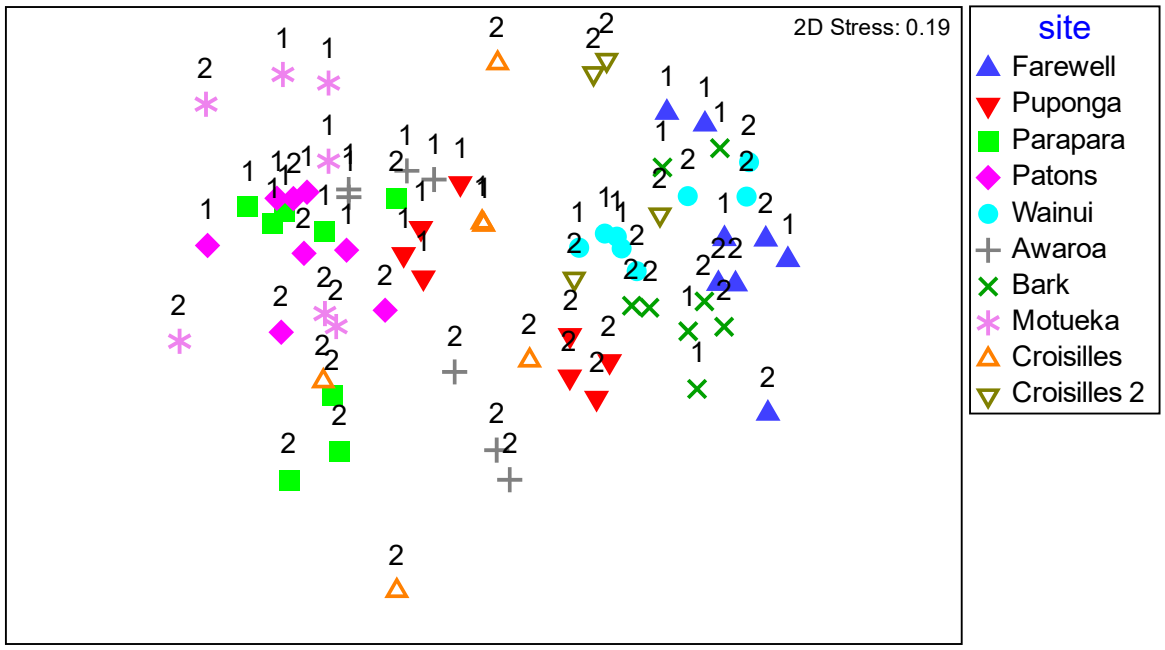

Figure 24: Non-metric MDS plot for benthic macrofaunal community data from scallop sites. Number represents sampling event 1 (June 2018) and 2 (December 2018). Samples with more similar community composition are positioned closer to each other in the plot.

Large epifauna

Video transects were completed in December 2018 at each of the experimental spat release study sites (but not at the additional survey site of Croisilles 2 due to time limitations) and analysed to quantify the density of conspicuous large epifauna (expressed as number of individuals per square metre) and the presence of different benthic features. Very poor visibility prevented quantification of benthic fauna at Parapara and Motueka, but habitat features were identified at all sites. Two transects were able to be analysed from Bark, four from Awaroa, and three from all other sites.

The large epifauna community composition data from the video transects were analysed to generate the MDS presented in Figure 25; this analysis included scallops, but the pattern was similar when scallops were excluded. The sites were clustered into two distinct groups in the ordination space, with Croisilles, Bark, Wainui, Farewell, and Puponga, the sandier sites, separated from Patons and Awaroa, two of the muddier sites, which were also distinct from each other. Species diversity was higher in the Croisilles, Bark, Wainui, Farewell, and Puponga group. The species driving the differences between the sites varied, but horse mussels (*Atrina zelandica*), hermit crabs (*Pagurus novizealandiae*), and starfish (*Coscinasterias muricata* and *Patiriella regularis*) were more abundant in the Croisilles, Bark, Wainui, Farewell, and Puponga group, and gastropods (including *Austrofusus glans* and *Cominella adspersa*) were more abundant at Patons, Awaroa, and Puponga. Heart urchins (*Echinocardium* sp.) were notably abundant at Patons.

Habitat features identified from the video did not distinctly separate sites, but the Croisilles, Bark, Wainui, Farewell, and Puponga sites had more structure-forming features (e.g., shells, shell hash, tubeworms, red and green algae), while the other sites had minimal benthic structure: Motueka and Parapara only had holes/burrows as an identifiable feature, Patons only had holes/burrows and diatom mats, and Awaroa had holes/burrows and diatom mats plus green algae, mixed shell, and faecal/psuedofaecal casts.

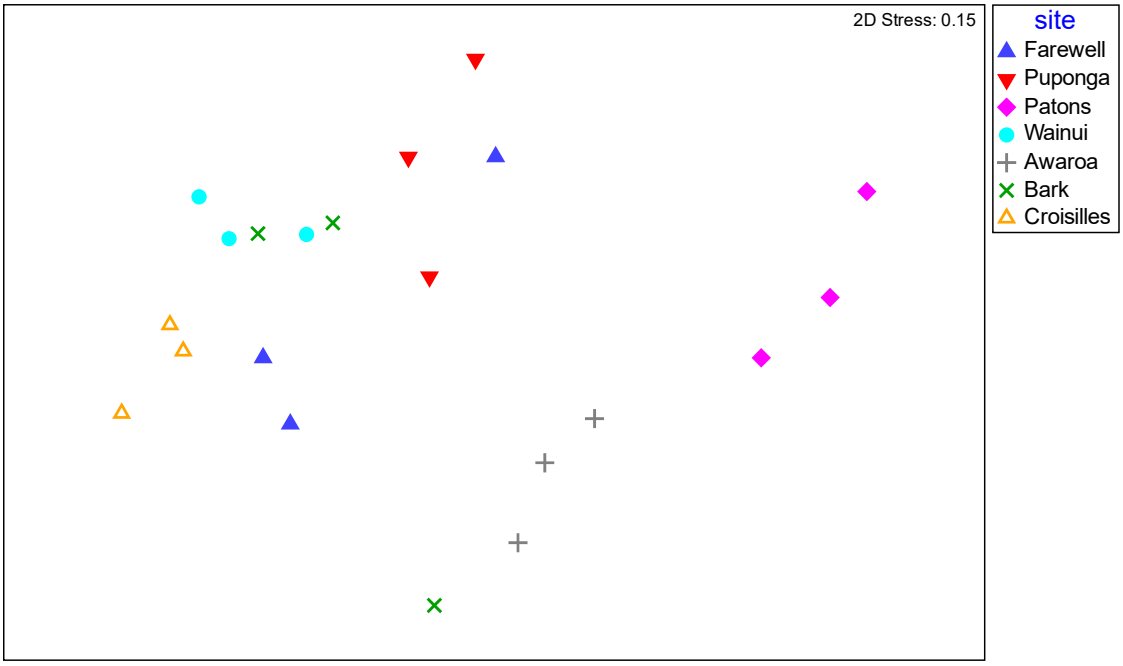

Figure 25: Non-metric MDS plot for video transect epifaunal community data from scallop sites surveyed in December 2018. Samples with similar community composition are positioned close to each other in the plot.

4.4 Scallop spat and habitat photos, and diver observations

Scallop spat were photographed at the time of marking in May 2018 to document the source of the spat released, and underwater photos of the seabed were taken while diving at three of the study sites (Bark, Croisilles 2, and Patons) in December 2018. A sample of the images taken is provided to illustrate the survival of scallop spat in suitable habitat at the Bark site (Figure 26) and to show the visually obvious differences in benthic conditions between the suitable sandy and heterogenous structured habitat at the Croisilles 2 site and the unsuitable and easily disturbed muddy and homogeneous habitat at the Patons site (Figure 27). Site characteristics and observations recorded during the dive sampling in June and December 2018 are summarised in Table 10.

Figure 26: Photos illustrating scallop spat and scallop bed habitat in Tasman Bay, 2018. Top: Juvenile scallops ('spat') used in the present study, sourced from commercial collector bags in May 2018. Bottom: Scallop bed habitat at the Bark Bay study site in Tasman Bay, December 2018; the noticeable shell mark on the scallop in the foreground indicates that it likely originated from the scallop spat deployment at the study site in May 2018. Photos by J. Williams (NIWA).

Figure 27: Photos taken in December 2018 illustrating differences in benthic habitat between two of the study sites. Top: Sandy scallop bed habitat at the Croisilles 2 site in Tasman Bay site in Tasman Bay. Bottom: Muddy habitat at the Patons site in Golden Bay that no longer supports scallops. Photos by J. Williams (NIWA).

Table 10: Site characteristics and observations recorded during diver sampling. Sites are ordered top to bottom with increasing scallop density (scallops < 80 mm m^{-2} in December 2018) (see Table 5).

Site	Visibility and current	Substrate	Structural habitat features	Conspicuous species noted
Parapara, GB	2 m	Mud	Little structure. Holes/burrows in soft mud.	Numerous predatory gastropods (e.g., knobbed whelks *Austrofusus glans*) and starfish (eleven-armed starfish *Coscinasterias muricata*) feeding on clumped scallop spat. Heart urchins (*Echinocardium cordatum*), small octopus (~100 mm, species unknown), hermit crabs (*Pagurus novizealandiae*).
Motueka, TB	1–2 m	Mud	Little structure. Holes/burrows in soft mud.	Little life. Hermit crabs (*Pagurus novizealandiae*), cushion stars (*Patiriella regularis*).
Awaroa, TB	Variable 2–6 m	Mud with very fine sand	Little structure. Diatom mats.	Little life. Hermit crabs (*Pagurus novizealandiae*), ascidians (*Cnemidocarpa* sp.), gastropods. Oyster (*Ostrea chilensis*). A large (~40 cm) blue cod (*Parapercis colias*) swam into one of the quadrats in June and tried to bite the bag of scallop spat collected. Lots of spotties (*Notolabrus celidotus*) around mooring line. Schooling jack mackerel (*Trachurus novaezelandiae*).
Patons, GB	2 m	Mud	Little structure. Holes/burrows in soft mud. Diatom mats.	Predatory gastropods (e.g., spiny murex *Poirieria zelandica*) and eleven-armed starfish (*Coscinasterias muricata*) feeding on clumped scallop spat. Heart urchins (*Echinocardium cordatum*). Spotties (*Notolabrus celidotus*) around mooring line.
Puponga, GB	1–2 m Notable current.	Fine sand and silt with broken shell.	Numerous solitary ascidians. Broken shell.	Abundant solitary ascidians (*Cnemidocarpa* sp.), sea cucumbers (*Australostichopus mollis*) and hermit crabs *Pagurus novizealandiae* (living inside turret shells *Maoriculpus roseus*). Eleven-armed starfish (*Coscinasterias muricata*) found on top of clumped scallop spat. Camouflage crab (*Notomithrax minor*), kina (*Evechinus chloroticus*), gastropods (Arabic volute *Alcithoe arabica*; knobbed whelk *Austrofucus glans*).
Farewell, GB	8 m Strong current.	Medium and fine sand with shells	Extensive tubeworm mounds and shell patches. Horse mussels.	Occasional large scallop (*Pecten novaezelandiae*). Numerous hermit crabs (*Pagurus novizealandiae*). Eleven-armed starfish (*Coscinasterias muricata*), large octopus (*Pinnoctopus cordiformis*). Gastropod eggs on shells. Horse mussels (*Atrina zelandica*). Schooling kingfish (*Seriola lalandi*).
Croisilles, TB	3–4 m	Very fine sand and silt	Diatom mats.	Scallop (*Pecten novaezelandiae*) bed. Eleven-armed starfish (*Coscinasterias muricata*), cushion stars (*Patiriella regularis*). A few hermit crabs (*Pagurus novizealandiae*). Finger sponge (*Callyspongia ramosa*). Gastropods (olive shells *Amalda australis*).
Wainui, GB	4 m	Fine sand with silt	Tubeworm patches. Shells. Horse mussels. Sunken driftwood.	Scallop (*Pecten novaezelandiae*) bed. Horse mussels (*Atrina zelandica*), kina (*Evechinus chloroticus*), gastropod eggs on *Atrina*, sea cucumbers (*Australostichopus mollis*). Eleven-armed starfish (*Coscinasterias muricata*) observed climbing up mooring line, and on top of a horse mussel (*Atrina zelandica*). Hermit crabs (*Pagurus novizealandiae*), octopus (*Pinnoctopus cordiformis*). Cushion star (*Patiriella regularis*) feeding on scallop spat. Clubbed tunicate (*Styela clava*). New Zealand sole (*Peltorhamphus novaezeelandiae*).
Bark, TB	4–5 m	Fine sand	Tubeworm mounds. Brown algae (likely *Dictyota ocellata*). Horse mussels.	Scallop (*Pecten novaezelandiae*) bed; scallops appear to be associated with tubeworm mounds. Sea cucumbers (*Australostichopus mollis*), eleven-armed starfish (*Coscinasterias muricata*), cushion stars (*Patiriella regularis*), horse mussels (*Atrina zelandica*), oysters (*Ostrea chilensis*), hermit crabs (*Pagurus novizealandiae*), kina (*Evechinus chloroticus*), camouflage crab (*Notomithrax minor*). Spotties (*Notolabrus celidotus*), juvenile blue cod (*Parapercis colias*), snapper (*Chrysophrys auratus*).
Croisilles 2	5–6 m.	Fine sand	Tubeworm mounds. Green algae (*Ulva* sp.) Horse mussels. Sponges.	Scallop (*Pecten novaezelandiae*) bed. Horse mussels (*Atrina zelandica*), sea cucumbers (*Australostichopus mollis*), cushion stars (*Patiriella regularis*), eleven-armed starfish (*Coscinasterias muricata*), hermit crabs (*Pagurus novizealandiae*), wandering anemone (*Phlyctenactis tuberculosa*), finger sponges (*Callyspongia ramosa*).

4.5 Modelling scallop survival, growth, and density in relation to environmental variables

There appear to be clear environmental variables characterising the environmental conditions (Figure 23) and the benthic macrofaunal (Figure 24) and large epifaunal (Figure 25) communities across the range of sites studied. Several of the environmental variables were strongly correlated with each other (correlation coefficients ≥ 0.7 or ≤ -0.7; see Figure 28 for correlations between most variables), therefore the sediment particle size variables of very fine sand, medium sand, and coarse sand (%), together with the sediment variables of softness, compressibility, and organic matter content, and the seawater variables of suspended solids, particulate nitrogen, and turbidity, were all excluded from the further analyses; however, the variables retained should be considered as proxies for those they are correlated with (Table 11). The modelling also did not include: water current speed and water clarity (as measured by Secchi readings), which were correlated with each other (0.7) and both were correlated with medium sand (correlations = 0.7–0.8); phaeophytin, which was not strongly correlated with any of the other variables (strongest correlation was 0.6 with both organic matter and particulate carbon) but is a derivative of chlorophyll *a*; and the previously identified covariates of suspended solids, volatile suspended solids, and inorganic suspended solids (correlations of 0.9 or 1.0 with each other). While depth varied between sites and will influence benthic conditions for scallops, we know all the sites examined have supported scallop populations in the past, therefore this term was retained for the modelling, on the assumption that depth has not changed since these sites supported scallops.

Table 11: Environmental variables retained for further analysis of scallop density, survival, and growth, and excluded variables that the retained variables should be considered proxies for. Abbreviations for each variable (as referred to in Figure 28) are shown in parentheses.

Retained variables	Positively correlated proxy	Negatively correlated proxy
% gravel (gravel)		
% mud (mud)	% organic matter (organic) sediment softness (soft.)	% fine sand (f.sand) % medium sand (m.sand) % coarse sand (c.sand) sediment compressibility (compr.)
Chlorophyll *a* sediment (chl a)		
Depth (depth)		% coarse sand (c.sand)
Seawater dissolved oxygen (DO)	% very fine sand (v.f.sand)	seawater suspended solids (ss) seawater particulate nitrogen (pn) seawater turbidity (turb)
Seawater particulate carbon (pc)	seawater turbidity (turb)	
Seawater chlorophyll *a* (chl)		% very fine sand (v.f.sand)

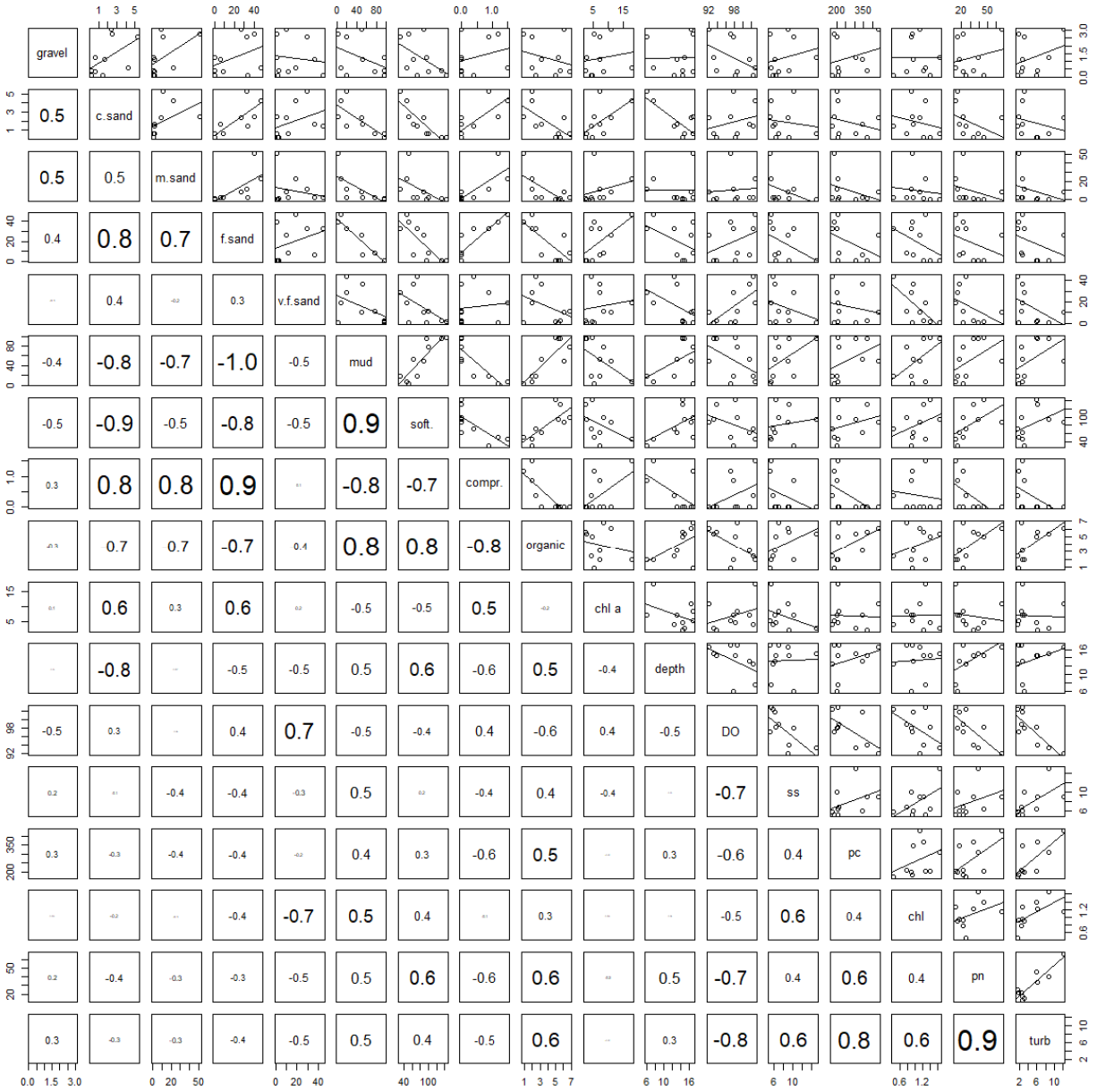

Figure 28: Pairs plot (scatterplots on upper right, correlation coefficients on lower left) for environmental variables. Environmental variable abbreviations are explained in Table 11. Font size emphasises the strength of the correlation coefficients.

Scallop survival and growth estimates were modelled in response to environmental parameters, to determine the strongest drivers. Difficulties in sampling at the Farewell site meant that the reseeded spat were not well sampled in June 2018 (and therefore survival and growth estimates involving the Farewell site June data are unreliable). No survival or growth data are available for the Croisilles 2 site (as no spat were released here and the site was only sampled at the December time point). Scallop survival was strongly correlated with recorded density in the December survey (Figure 29), and so density was also examined as a response variable.

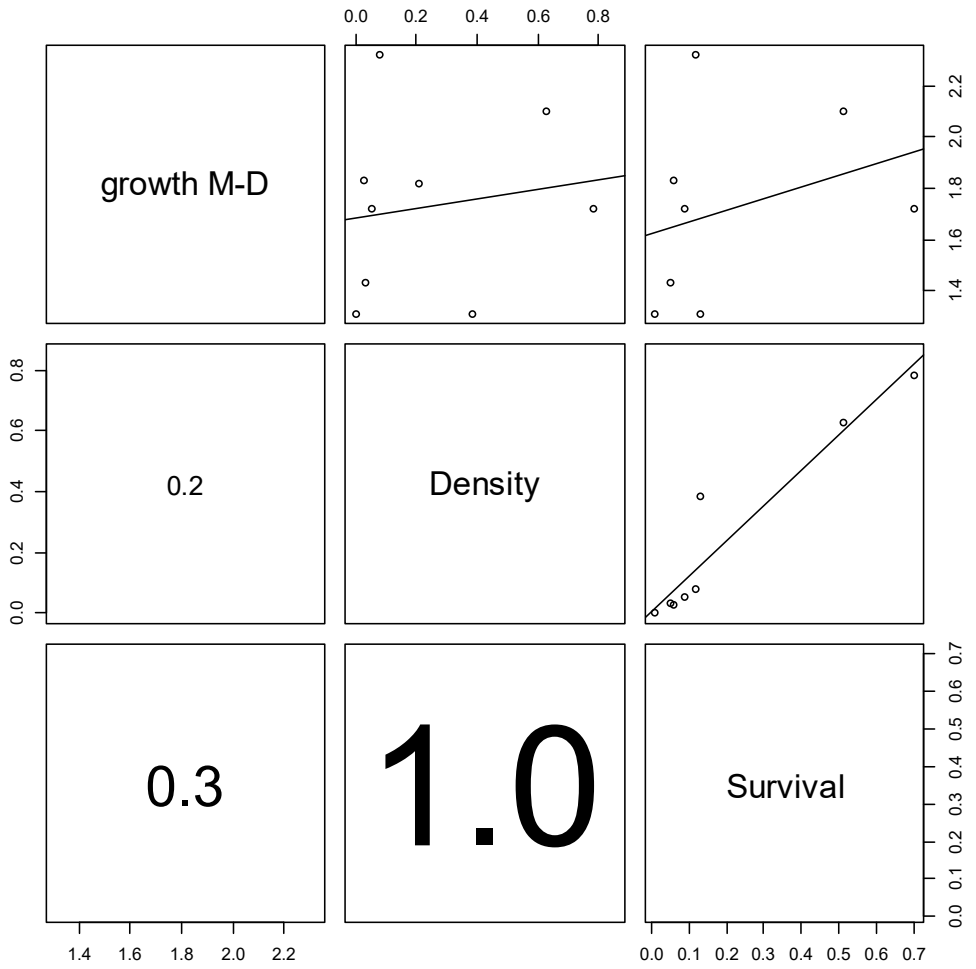

Figure 29: Pairs plot (scatterplots on upper right, correlation coefficients of lower left) for scallop parameters. Growth M-D = growth between May and December 2018. Font size indicates the strength of the correlation coefficients.

Scallop growth

Following model selection (AIC based), the final model retained the terms of sediment chlorophyll *a*, depth, dissolved oxygen, and chlorophyll *a* in the water as explanatory terms explaining 28% of the variability; however none of these terms were significant at the P = 0.05 level (Table 12).

Table 12: Analysis of variance table for final model examining relative scallop growth.

	Df	Sum sq	Mean sq	F value	Pr (> F)
Chlorophyll *a* (sediment)	1	0.0517	0.0517	0.6102	0.4784
Depth	1	0.0099	0.0099	0.1163	0.7502
Dissolved oxygen (seawater)	1	0.4039	0.4039	4.7662	0.0944
Chlorophyll *a* (seawater)	1	0.1417	0.1417	1.6715	0.2657
Residuals	4	0.3390	0.0847		

Starting with the same initial model but excluding depth, backwards and forwards stepwise model selection resulted in a final model retaining terms for sediment mud content (%) and dissolved oxygen. These terms explained 34% of the variability. Again, neither of the terms were significant at the P = 0.05 level (Table 13).

Table 13: Analysis of variance table for final model (depth excluded) examining relative scallop growth.

	Df	Sum sq	Mean sq	F value	Pr (> F)
% mud	1	0.1363	0.1363	1.7383	0.2355
Dissolved oxygen	1	0.3392	0.3392	4.3251	0.0828
Residuals	6	0.4706	0.0784		

Scallop survival

Scallop survival was modelled against the same environmental explanatory variables as used for scallop growth (i.e., sediment chlorophyll *a*, phaeophytin, % mud, % gravel, depth, dissolved oxygen, particulate carbon, and water column chlorophyll), within a generalised linear modelling framework and a beta error distribution, with model selection using a backwards and forwards stepwise approach. The final model retained terms for chlorophyll *a* in the sediment, chlorophyll *a* in the water, and depth and had a pseudo r^2 of 0.94. Sediment chlorophyll *a* and depth were both significant at the 5% level (Table 14), having positive and negative effects, respectively, on survival.

Table 14: Model outputs summary for final model examining scallop survival. Significant p values highlighted in bold.

	Estimate	Std. error	t value	Pr (> t)
(Intercept)	1.5384	0.7913	1.944	0.1471
Chlorophyll *a* sediment	0.1583	0.0330	4.798	**0.0172**
Depth	-0.2513	0.0361	-6.967	**0.0061**
Chlorophyll *a* seawater	-1.2489	0.5913	-2.112	0.1251

Starting with the same initial model but excluding depth, the final model had a pseudo r^2 of 0.91 and only retained terms for the % mud and % gravel in the sediment, with % mud showing a strong negative correlation with scallop survival (Table 15).

Table 15: Model outputs summary for final model (depth excluded) examining scallop survival. Significant p values highlighted in bold.

	Estimate	Std. error	t value	Pr (> t)
(Intercept)	1.4364	0.4182	3.434	0.0264
% mud	-0.0509	0.0061	-8.305	**0.0012**
% gravel	-0.2476	0.1709	-1.449	0.2211

Scallop density

Scallop density in December 2018 was considered a proxy for scallop survival, which enabled inclusion of data from the Farewell and Croisilles 2 sites (i.e., because the survival estimate for Farewell was excluded due to its unreliability, and a survival estimate was not available for Croisilles 2 which was sampled only in December 2018). Density was modelled against the selected environmental variables (sediment chlorophyll *a*, phaeophytin, % mud, % gravel, depth, and water column dissolved oxygen, particulate carbon, and chlorophyll) using the same model selection process. Terms for sediment chlorophyll *a*, % mud, % gravel, depth and particulate carbon were retained in the final model, with an r^2 of 0.89 (Table 16). Sediment chlorophyll *a*, % mud and % gravel and depth were all significant at P = 0.05. Sediment mud content (%) had the strongest effect (P = 0.004).

Table 16: Analysis of variance table for final model examining scallop density. Significant p values highlighted in bold.

	Df	Sum sq	Mean sq	F value	Pr (> F)
Chlorophyll *a* sediment	1	0.1691	0.1691	14.0493	**0.0200**
% mud	1	0.4236	0.4236	35.1963	**0.0040**
% gravel	1	0.2073	0.2073	17.2209	**0.0143**
depth	1	0.1326	0.1326	11.0124	**0.0294**
particulate carbon	1	0.0210	0.0210	1.7439	0.2571
Residuals	4	0.0482	0.0120		

Excluding depth from the terms in the initial model resulted in a final model retaining only sediment mud content (%) and gravel content (%), with an r^2 of 0.74 (Table 17).

Table 17: Analysis of variance table for final model (depth excluded) examining scallop density. Significant p values highlighted in bold.

	Df	Sum sq	Mean sq	F value	Pr (> F)
% mud	1	0.5916	0.5916	20.5272	**0.0027**
% gravel	1	0.2084	0.2084	7.2307	**0.0311**
Residuals	7	0.2017	0.0288		

5. DISCUSSION

Investigating scallop responses to habitat factors

This study represents the first large scale scientific field experiment to examine the fate of reseeded *Pecten novaezelandiae* scallop spat in relation to environmental and ecological habitat factors in New Zealand. We quantified scallop size frequency, spatial density, and body condition, and estimated the survival and growth of experimentally released scallop spat, across a range of sites with contrasting habitat characteristics in Golden Bay and Tasman Bay at the north of New Zealand's South Island. We linked these scallop biological variables to environmental sediment and seawater variables and to ecological benthic community data that are anticipated to influence scallop population dynamics. Such habitat features are likely to have multiplicative effects, with aspects detrimental to scallop survival and growth interacting across environmental and ecological gradients, along with additional external stressors, such as pollution, disease, and weather events (Thrush et al. 2008). Our analysis aimed to identify indicators of habitat suitability for scallops.

Differential scallop size, density, and survival

Clear differences in scallop size, density, and survival were observed among sites, indicating that habitats were substantially more suitable at some sites than others. Larger scallops were present only at five sites (the experimental sites of Farewell, Croisilles, Wainui, and Bark, and the additional survey site of Croisilles 2), signifying that conditions at these sites had been sufficiently favourable for the survival and growth of naturally settled spat to attain these larger sizes by the time of our 2018 field study. At the end of our study, the densities of smaller scallops (< 80 mm in December, assumed to be predominantly from our experimental releases in May) and the estimates of spat survival were highest at these same sites (noting survival was not estimated at Croisilles 2 because spat were not experimentally released there). These sites of previous particular importance to the scallop fishery appeared to still be appropriate for supporting scallop survival and growth in 2018. The absence of larger scallops at the other sites (Parapara, Motueka, Awaroa, Patons, and Puponga) could indicate that either natural spat settlement in these areas had not occurred in the period leading up to our study or

that the habitats were unsuitable. Our findings of low scallop densities and minimal survival at these sites provides evidence supporting the latter.

Environmental indicators of habitat suitability

Sites with larger, presumably wild, scallops and the highest densities and survival of smaller scallops had similar environmental characteristics, including firmer sediments with high fine sand and very fine sand content, low mud and organic matter content, and generally higher levels of chlorophyll *a*, and seawater with high dissolved oxygen and generally lower suspended solids concentrations. These were amongst the environmental variables identified as important determinants of habitat suitability. Although we found no significant effect of any of the measured environmental variables on scallop growth, our final modelling identified significant relationships with scallop density and survival: density was significantly negatively affected by sediment mud content and gravel content, and survival was significantly negatively affected by sediment mud content. In our initial modelling, depth was included and retained as a significant term influencing scallop density and survival, but the relationships between depth and scallop density and survival were unclear: although density and survival were high at the two shallowest sites (Bark and Wainui), density was higher at a deeper site (Croisilles 2). It is well known that depth is correlated with other benthic characteristics, such as sediment type and benthic primary production (Nelson et al. 1999, Gillespie et al. 2000) and community faunal species composition and functional composition (Bolam et al. 2017), and depth itself is unlikely to be a causal factor influencing scallops (Brand 2016). While the habitat suitability for scallops appears to have changed since the times when all our study sites supported healthy scallop beds, site depth has not changed. For these reasons, depth was excluded as a variable in our final modelling.

Several environmental variables were highly correlated. For example, sediment mud content was negatively correlated with the covariates of sediment sand content and compressibility, and positively correlated with organic matter content and sediment softness. Likewise, seawater dissolved oxygen was positively correlated with sediment very fine sand content and negatively correlated with seawater suspended solids, particulate nitrogen, and turbidity. These terms were excluded from the final modelling as covariates (Zuur et al. 2009), but it is important to recognise the collinearity and consider that it might well be one or more of the excluded terms that is responsible for the effect, rather than the terms included in the modelling. In particular, some of these correlated variables have been previously identified as important drivers of *P. novaezealandiae* scallop population dynamics, with higher scallop densities linked to sandy sediments (Willan 1981, Morrison 1999, Taylor & Morrison 2008) and decreased survival and growth linked to elevated levels of suspended sediments (Stevens 1987, Thrush et al. 1995, Nicholls et al. 2003).

Ecological indicators of habitat suitability

All sites were dominated by benthic macrofauna (infaunal and epifaunal species) typical of sandy–muddy sediments, but the sites with the highest scallop spat densities and survival rates—Croisilles 2 (density only), Bark and Wainui, (density and survival)—had higher abundances of bivalves, hermit crabs, and starfish. These more suitable sites also had higher habitat complexity due to the presence of more shell material and structure-forming epifauna including horse mussels and small-sized species of polychaete worms which build their tubes out of fine sediments. Scallops were often found to be associated with such tubeworm patches or mounds. The small tubes of these polychaetes may be suitable settlement surfaces for scallop larvae to attach to, and they may provide refuge from predators. However, it should be noted there have been increased densities of potentially invasive large-bodied tubeworms (proposed species: *Chaetopterus chaetopterus*-A (Geoff Read, pers. comm.) observed elsewhere (i.e., in the Marlborough Sounds) (Williams et al. 2019, Williams et al. 2021, Williams et al. 2024a) and, despite the significant structural habitat complexity they provide, these types of large-sized tubeworms may suppress scallop settlement and survival due to competition for physical space on the seafloor and phytoplanktonic food. Those sites with the lowest densities and survival rates—Parapara, Motueka, Awaroa, and Patons—were characterised by soft, muddy, easily disturbed sediments, with only burrows (Parapara and Motueka), diatoms (Awaroa), or burrows and diatoms (Patons) as their distinguishing features, leading to a low habitat complexity. Low habitat complexity may result in increased predation on the scallop spat due to lack of shelter and refuges (Talman et al. 2004).

Experimental spat release and sampling considerations

This study indicates benthic and water column related factors that may be important in determining the habitat suitability of the selected sites in the Golden Bay–Tasman Bay region. However, it is difficult to assess the effects of multiple environmental and ecological factors on scallop survival and growth over short time periods (such as the seven months over which this field experiment was undertaken) and longer time periods, and there are some limitations in this study that may have confounded the results.

Remote deployment of scallop spat from the survey vessel limited our control over fine-scale release locations, potentially resulting in variability among sites in the spatial density (patchiness) of the released spat. The timing of spat deployments in relation to tidal phases varied among sites which could have influenced the magnitude of spat dispersal. While not possible within this work due to budget constraints, spat release by divers on the seabed would provide far better control in achieving homogeneous release densities within and among sites and precise deployment locations to improve the chances of accurately relocating animals in subsequent diver sampling. Our quadrat-based estimates depend on our ability to resample the same scallop populations released. During the spat deployment at the Farewell site strong currents caused the vessel to drift away from the marker buoy. While subsequent diver sampling tried to take account of this drift, it is possible that the Farewell deployment site was not well sampled, as the estimated June scallop density appears to be an underestimate relative to the December estimate. However, the fact that scallops were recovered on both occasions indicates the Farewell site had favourable conditions conducive for scallop survival.

One potential reason for the observed declines in scallop densities is that there could have been significant short-term events that caused mortality that were not captured in the data collection. Environmental sampling was only possible on two occasions, in June and December, approximately three weeks and seven months after scallop spat were experimentally released. While benthic sediment composition was relatively consistent between dates, point sampling of seawater variables such as suspended sediment concentration are unlikely to be representative of the conditions experienced at the site over the longer term. Ideally, environmental variables would be measured (semi-) continuously between multiple sampling time points to capture temporal environmental variability and any acute events (e.g., algal blooms, weather/storm events elevating near-seabed turbidity) that may affect scallop health and mortality. Differences in the benthic sediment characteristics and communities between sites are probably a better reflection of differences in environmental conditions prevailing over the longer term. In particular, the benthic community is a good proxy for the overall conditions at a site, because the organisms present are exposed to, and are responding to, the combined benthic and water column conditions the entire time.

Studying a greater number of experimental sites (e.g., 15–25) may have been beneficial for capturing a wider variety of environmental and ecological states across many differentially suitable habitats, but this was not possible within the project resources, plus we failed to find any other existing scallop beds within diveable depths in Golden Bay and Tasman Bay during our additional exploratory towcam video camera work. The Adele site marker went missing meaning this site could not be sampled after spat release; however, an extra site (Croisilles 2) which had not received spat deployments was included and surveyed in the study to provide additional data for comparison with the nine experimental sites. Although our study used only 10 sites overall, there was great contrast in the environmental and ecological states across these sites, which was sufficient for detecting significant environmental effects affecting scallop responses. Sampling also had to be conducted within a limited time (one dive per site per sampling event) and particularly poor underwater visibility resulted in fewer quadrats sampled than planned at most sites. More replicates of quadrats and other samples likely would have increased the accuracy and precision of our estimates.

Scallop mortality and movement

Estimated densities of spat recovered during the June and December samplings were markedly lower than the estimated release densities. This decline is hypothesised to reflect both mortality and spat

dispersal beyond the study sites. Scallop spat are typically more mobile than larger juveniles and adults, with scallops adopting an increasingly sedentary lifestyle as they grow larger (Brand 2016). It is predicted that given their smaller size, the spat released in our study were more likely to move within and potentially outside the release plot areas in June than when they had grown larger by December. While more dispersal could have occurred early on be responsible for some of the initial decline in density, we assumed there were no differences among sites in this potential ontogenetic effect on scallop dispersal. However, it should be noted that our survival (and mortality) estimates were calculated assuming there was no movement of spat outside the spat release areas at each site, so they likely underestimate true survival (and overestimate true mortality). The estimates were derived from relatively small sample sizes, which were the largest that could be achieved within the limitation of a single dive at each site on each sampling event. Increased replication in future studies is recommended, to improve the precision of the estimates calculated.

There was no difference in spat mortality and length distribution between the before-and-after calcein treatment so we are confident that the spat released were unaffected by calcein staining and were healthy and representative of a natural cohort with no unusual detrimental health issues. Based on the May spat release and June dive sampling data, less than 20% of spat at each site had survived this initial three-week period following release, except at Croisilles and Parapara where about 50% had survived. Survival of the remaining spat between June and December (7 months) was relatively high at the sites with more favourable habitat characteristics (Bark and Wainui) but was much lower at Croisilles and the other experimental sites with apparently low habitat suitability. This suggests that although initial mortality of spat was high at most sites, later mortality was low in suitable habitats.

Existing estimates of mortality rates in the SCA 7 fishery region are relatively high compared with other regions (Fisheries New Zealand 2022). The annual natural mortality rate for two populations of scallops in the Pelorus Sound was estimated to be 23% (instantaneous mortality rate $M = 0.26$) and 39% ($M = 0.49$) (Bull 1976). From a 1991–92 tagging study in Golden and Tasman Bay, young scallops (0+ and 1+ year classes) were estimated to have an annual natural mortality of 38% ($M = 0.21$), increasing to 66% ($M = 0.46$) in older scallops (year classes 2+) (Bull & Drummond 1994). This seems unusual because we would expect the younger scallops to have higher rates of mortality than the older scallops. Nevertheless, these estimates certainly indicate that a substantial natural loss of the reseeded individuals is to be expected, even at sites with suitable habitats. At the sites with the most suitable habitats in the present study, the June to December estimates of proportional mortality (30% at Bark and 49% at Wainui) were comparable with those estimated by Bull & Drummond (1994), even when the rates were annualised (51% at Bark and 74% at Wainui). However, we suggest that the actual mortality rates that occurred during in our study were lower than those estimated due to dispersal of some spat to areas outside of the study plots, hence we consider our estimates of mortality are overestimated. Current mortality rates of scallops could be expected to be higher than those of scallops living decades ago, due to the degradation of habitat suitability.

Potential sources of mortality

Potential sources of mortality include starvation, suffocation, predation, and disease. Unfavourable environmental conditions could result in acute mortality events (e.g., mortality from smothering and burial by sediments resuspended and deposited during and after storms). Incidences of large-scale die-offs in localised areas have been observed previously (e.g., mortality associated with storms in 1998) (Fisheries New Zealand 2022).

Initial predation by invertebrates and fish likely occurred soon after the spat deployments. During dive sampling in June 2018, three weeks after the experimental spat were released, predatory gastropods (including knobbed whelks *Austrofusus glans* and spiny murex *Poirieria zelandica*) and starfish (eleven-armed starfish *Coscinasterias muricata* and cushion stars *Patiriella regularis*) were observed to be feeding on scallop spat, especially on the clumps of spat attached to each other by byssus threads which were particularly prevalent at the Parapara and Patons sites. This kind of initial invertebrate predatory response to reseeded scallop spat has also been observed in northeastern New Zealand (Morrison 1999). Fish predation was not investigated in the present study, but we suspect fish predation

on the spat released may have been high. Potential fish predators of scallop spat observed during the dive sampling included blue cod (*Parapercis colias*), snapper (*Chrysophrys auratus*), spotties (*Notolabrus celidotus*), and New Zealand sole (*Peltorhamphus novaezeelandiae*). During a dive at the Awaroa site, a blue cod was observed to swim into a quadrat search area and attempt to eat the scallop spat that had been collected and bagged by the divers. Snapper are known to have increased in abundance in recent years (MacGibbon 2019) and could be a significant predator of small scallops.

The disease burden of scallops sampled in the present study showed no clear patterns among sites with scallop density and survival, suggesting disease did not appear to be a conspicuous factor influencing the scallop populations. However, of the scallop condition and disease data collected, most data were derived from scallops sampled at sites where wild scallops were found. As such, there is a survivorship bias in these data and we do not know the overall condition or disease burden of scallops at the sites where wild scallop numbers and seeded spat scallop recovery was low.

Scallop growth

No detectable growth, as measured through changes in the overall length distribution, was observed in the experimental scallop spat between the middle and the end of May, when the spat were being held prior to experimental release. This likely reflects the inability of comparing length distributions as an approach for detecting growth over such a short period. Alternatively, growth may have been supressed resulting from stress caused by the spat handling processes. The slight increase (of ~7 mm) in the median shell length of small scallops between the end of May (the time of release) and June (the time of quadrat sampling) indicates a small amount of growth occurred during this three-week period. The clear difference in the modal length range of small scallops recovered during the quadrat sampling (10–50 mm in June and 40–80 mm in December) suggests significant growth (an increment of ~ 33 mm, 122% of the initial shell length) occurred during this seven-month period. Growth was estimated using the change in median size, a metric less affected by outliers than the mean, but we cannot know whether there was any size-related mortality or differential growth. Although some of the small scallops sampled could have been from natural settlement in the wild, we expect most originated from our experimental spat release in May.

Comparison of scallop growth estimates among sites in our analysis was based on the difference between the median sizes of spat released in May and recovered in December. This method was different to that in the experimental design, in which we had intended to track the growth of individuals, hence the use of the calcein marking treatment. While the released spat had been marked with calcein stain, enabling individual growth increments to be measured, measuring this was prohibitive within the project time and cost budget. Preliminary investigations of a sample of the calcein-treated scallop spat revealed the presence of calcein marks in the external shell surfaces was variable, but shell sectioning was more effective at detecting the marks. Unfortunately, further investigation of individual scallop shells was not feasible within the available project resources (although the shells were saved, and individual growth potentially could be estimated in future studies). This means that the growth estimated from changes in median size could potentially be confounded with site differences in size related mortality (i.e., sites with relatively higher mortality of smaller spat would end the experiment with a larger median size, and so have a greater apparent growth), and our measure of relative growth may be a poor measure of individual scallop growth.

Changing scallop habitats

The habitats surveyed once supported a thriving scallop fishery (Williams et al. 2014). The observed large declines in the scallop populations (Williams et al. 2014, Williams et al. 2021) could be due to a range of factors (see review by Hale et al. 2024). The environmental conditions and/or benthic environment could have changed significantly from past conditions when scallops were thriving. This we cannot determine due to lack of previous baseline information. Land-based sedimentation has likely increased the silt and clay (mud) content of the marine sediments in certain areas in the Golden Bay–Tasman Bay region, and elevated levels of suspended sediment concentrations have also been observed. Previous dredging activity may have altered the habitat complexity and benthic community structure (Handley et al. 2014, Handley et al. 2020). The form and extent of benthic habitat restructuring is

dependent on sediment type, with cohesive muddier sediments showing detrimental effects even at low frequencies of dredging, while sandier sediments may be more resilient to benthic community alteration at low benthic disturbance frequencies (Pommer et al. 2016, Hale et al. 2017). Differential vulnerability of longer lived (Rijnsdorp et al. 2018), and potentially biogenic habitat forming, species means that both the benthic faunal community and habitat complexity may be altered and recovery periods may be slow (Kaiser et al. 2006), or there may be a tipping point beyond which the benthos, and consequently the scallop population, does not recover.

Conclusion

In general, modelling of scallop responses to environmental variables in our 2018 field study suggested that scallop density and survival are influenced by seabed parameters and that growth may be influenced more by seawater parameters. These findings are to be expected given the sedentary benthic lifestyle and suspension feeding mode of scallops. The sites in our study that supported extant scallop populations, and that supported the survival and growth of the experimentally released scallop spat, were characterised by several consistent environmental patterns including low sediment mud content, low sediment organic carbon content, and higher seawater dissolved oxygen concentrations, plus were associated with higher benthic structural complexity. This knowledge could be used to identify potential candidate sites for restoration and reseeding efforts. However, we recognised that more field sampling would be required to see if the habitat suitability patterns identified also exist outside of the relatively sheltered bays of Golden Bay and Tasman Bay, and that future research should seek to investigate scallop-habitat relationships further.

Subsequent research

Following on from our 2018 experimental field study, two successive empirical studies were carried out to help advance our understanding of *P. novaezelandiae* scallop-habitat relationships: 1) a laboratory experiment in 2020 (Moss et al. 2023); and 2) field survey sampling in 2021 (Williams et al. 2024a, Williams et al. 2024b) followed by sample processing and analysis (Hale et al. 2024).

The laboratory experiment in 2020 investigated the effects of elevated suspended sediment concentrations (SSCs) on scallop spat (using spat and sediment collected from a Motueka site in Tasman Bay), which provided some useful insights into their tolerances to this stressor (Moss et al. 2023). The experiment showed that scallop clearance rates (the weight of suspended sediment removed per scallop per hour) and righting response (when turned upside down, scallops clap their valves to resume their preferred orientation) were both affected after exposure to elevated SSCs. Faster sediment clearance rates were observed with increasing SSC up to about 500–600 mg L^{-1} above which clearance rates were reduced, suggesting the scallops actively responded to the elevated SSCs but had difficulty processing the sediments in the highest SSC treatments. These findings were similar to those of Nicholls et al. (2003) whose experiment on larger scallops found that over time the scallops in the higher suspended sediment treatments had a lower filtration rate than the controls. The righting response in the Moss et al. (2023) experiment in 2020 was faster in SSCs > 200 mg L^{-1}, which may be the result of shell valve clapping to clear unwanted particles from the gills and feeding apparatus as fast as possible in the higher SSCs, a behavioural mechanism suggested by Nicholson (1978). The 2020 scallop SSC tolerance experiment was cut short due to COVID-19 restrictions, limiting the experiment to just 16 days instead of the planned four weeks. Further experimental work was recommended to determine the effects of longer-term exposure to elevated SSCs on scallop physiology, including studies of smaller spat which may be more vulnerable (Moss et al. 2023).

In 2021, dive transect surveys of scallops were conducted at key scallop bed locations in northeastern North Island (Williams et al. 2024b) and in Marlborough Sounds in northern South Island (Williams et al. 2024a), enabling the collection of scallop-habitat field data and samples across a much wider range of scallop bed sites than those used in our 2018 study in Golden Bay and Tasman Bay (present study). The divers made observations of scallop size and density and collected images and samples, including sediment and macroinvertebrate core samples, along each transect. The newly collected data and samples from 230 sites in the 2021 dive surveys (Williams et al. 2024a, Williams et al. 2024b) were processed and analysed within a separate project that investigated the cumulative effects of stressors on

scallops and scallop habitats (Hale et al. 2024). Relationships between scallop abundance and site characteristics (sediment coarseness and microalgal pigment content, habitat structural complexity, and macrofaunal community characteristics) were investigated using maximum density regression models. The analysis highlighted relationships between scallops and their environment, including sets of conditions where scallop densities were at their maximum, enabling better definition of what constitutes 'good' scallop habitat for *P. novaezelandiae* (Hale et al. 2024). Scallops were more abundant in sediments dominated by fine and very fine sands, and scallop density was weakly positively correlated with seafloor habitat complexity. Sites with high relative abundance of macrofaunal functional groups known to oxygenate sediments, build and occupy tubes in the sediment (bioirrigators, biodiffusers, surface modifiers), and to suspension feed, tended to have higher densities of scallops. Scallop density was negatively correlated with sediment softness and muddiness. The results of the Hale et al. (2024) analysis concur with the findings of our scallop habitat knowledge review and strongly support the results of our 2018 spat survivorship study in Golden and Tasman Bay (present study).

6. POTENTIAL RESEARCH

Hale et al. (2024) made the following recommendations for future research:

- collation of higher resolution data to link specific land and coastal activities to scallop declines;
- inclusion of new data and understanding into conceptual modelling projects;
- investigation of other environmental factors linked with seafloor ecosystem and scallop health;
- trialling methods for restoration and rehabilitation of scallops and/or scallop habitat;
- monitoring scallop spat in the water column at strategic sites, to investigate the relative importance of larval supply versus lack of suitable habitat for spat settlement and survival.

In relation to those recommendations, some further specific potential research ideas are provided below:

- Given the potential for predation to be a significant factor affecting scallop survival, future studies to investigate invertebrate and fish predation of scallops would be beneficial. Field methods could include the use of baited pots and underwater cameras to observe and quantify predation levels.
- Examining additional scallop-habitat related benthic and water column parameters in future work could be useful. Given the proposed importance of seawater dissolved oxygen, further investigations should perhaps consider other oxygen-related metrics, such as sediment community oxygen consumption, sediment oxygen penetration and redox depth.
- Functional benthic community processes could also be investigated, such as benthic carbon and nutrient cycling. For carbon this would include quantification of particulate organic carbon (POC) fluxes. Sinking POC transports carbon from the water column to the benthos and plays a large role in the marine and global carbon cycle, despite its small pool size (Legendre 1990, Prentice et al. 2001). For nitrogen this would include quantification of nitrogen-species porewater profiles and sediment-water interface flux. These processes have the potential to provide more information on the driving factors that maintain suitable habitat for scallops including feedback loops as scallops alter their habitat (Yang et al. 2021).
- Other variables that could be investigated include those related to bed stability and mud content— particularly those related to microphytobenthos biomass, a potential food source and sediment stabiliser. Sediment surface (top 1 mm) contact cores could be used to measure chlorophyll *a* concentrations and extracellular polymeric substances (ESPs, natural polymers of high molecular weight secreted by microorganisms into their environment), and a pulse-amplitude modulated (PAM) fluorometer could be used to measure minimum fluorescence, a proxy for microphytobenthos biomass (Honeywill et al. 2002, Jesus et al. 2006), and the maximum quantum yield of photochemical energy conversion in photosynthesis, a proxy for microphytobenthos 'health' (Maxwell & Johnson 2000).

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8. REFERENCES

Allen, D.M.; Costello, T.J. (1972). The calico scallop, *Argopecten gibbus*. Special Scientific Report – Fisheries Series 656. National Marine Fisheries Service, National Oceanic and Atmospheric Administration. 19 p.

Allen, J.A. (1953). Observations on the epifauna of the deep-water muds of the Clyde Sea area, with special reference to *Chlamys septemradiata* (Müller). *Journal of Animal Ecology 22*: 240–260.

Arsenault, D.J.; Girard, P.; Himmelman, J.H. (1997). Field evaluation of the effects of refuge use and current velocity on the growth of juvenile Iceland scallops, *Chlamys islandica* (O.F. Müller, 1776). *Journal of Experimental Marine Biology and Ecology 217*: 31–45.

Begon, M.; Harper, J.L.; Townsend, C.R. (1990). Ecology: Individuals, Populations and Communities. Blackwell Science, Cambridge, U.K. 945 p.

Belding, D.L. (1931). The scallop fishery of Massachusetts – including an account of the natural history of the common scallop. *Marine Fisheries Series 3* 51 p.

Bolam, S.G.; Garcia, C.; Eggleton, J.; Kenny, A.J.; Buhl-Mortensen, L.; Gonzalez-Mirelis, G.; van Kooten, T.; Dinesen, G.; Hansen, J.; Hiddink, J.G.; Sciberras, M.; Smith, C.; Papadopoulou,

N.; Gumus, A.; Van Hoey, G.; Eigaard, O.R.; Bastardie, F.; Rijnsdorp, A.D. (2017). Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Marine Environmental Research 126*: 1–13.

Bourgeois, M.; Brethes, J.C.; Nadeau, M. (2006). Substrate effects on survival, growth, and dispersal of juvenile sea scallop *Placopecten magellanis* (Gmelin 1791). *Journal of Shellfish Research 25*: 43–49.

Bourne, N. (1964). Scallops and the offshore fishery of the Maritimes. Fisheries Research Board of Canada Bulletin No. 145. 60 p.

Brand, A. (2016). Scallop Ecology: Distributions and Behaviour. *In*: Shumway, S.E.; Parsons, G.J. (eds.) *Scallops: Biology, Ecology, Aquaculture, and Fisheries*, pp. 469–533. Elsevier, Amsterdam.

Brand, A.R.; Paul, J.D.; Hoogesteger, J.N. (1980). Spat Settlement of the Scallops *Chlamys Opercularis* (L.) and *Pecten Maximus* (L.) On Artificial Collectors. *Journal of the Marine Biological Association of the United Kingdom 60*: 379–390.

Brown, C.J.; Sameoto, J.A.; Smith, S.J. (2012). Multiple methods, maps, and management applications: Purpose made seafloor maps in support of ocean management. *Journal of Sea Research 72*: 1–13.

Bull, M.F. (1976). Aspects of the biology of the New Zealand scallop, *Pecten novaezelandiae* Reeve 1853, in the Marlborough Sounds. Unpublished PhD thesis. Victoria University of Wellington, New Zealand. 175 p.

Bull, M.F.; Drummond, K.L. (1994). Report on Tasman Bay and Golden Bay scallop mortality trials. Central Fisheries Region Internal Report No. 24. 17 p.

Caddy, J. (1989). A perspective on the population dynamics and assessment of scallop fisheries, with special reference to the sea scallop, *Placopecten magellanicus* Gmelin. *In*: Caddy, J. (ed.). *Marine Invertebrate Fisheries: Their Assessment and Management*, pp. 559–589. John Wiley & Sons, New York, NY.

Caddy, J.F. (1972). Progressive loss of byssus attachment with size in the sea scallop, *Placopecten magellanicus* (Gmelin). *Journal of Experimental Marine Biology and Ecology 9*: 179–190.

Carey, J.D.; Wahle, R.A.; Stokesbury, K.D.E. (2013). Spatial scaling of juvenile-adult associations in northwest Atlantic sea scallop *Placopecten magellanicus* populations. *Marine Ecology Progess Series 493*: 185–194.

Christophersen, G.; Strand, Ø. (2003). Effect of reduced salinity on the great scallop (*Pecten maximus*) spat at two rearing temperatures. *Aquaculture 215*: 79–92.

Claereboudt, M.R.; Bureau, D.; Côté, J.; Himmelman, J.H. (1994a). Fouling development and its effect on the growth of juvenile giant scallops (*Placopecten magellanicus*) in suspended culture. *Aquaculture 121*: 327–342.

Claereboudt, M.R.; Himmelman, J.H.; Côté, J. (1994b). Field evaluation of the effect of current velocity and direction on the growth of the giant scallop, *Placopecten magellanicus*, in suspended culture. *Journal of Experimental Marine Biology and Ecology 183*: 27–39.

Cole, R.; Horn, P.L.; Davey, N.; Bradley, A. (2006). An estimate of the recreational catch of scallops and dredge oysters in the Golden Bay and Tasman Bay sections of the Southern Scallop Fishery (SCA 7) for the 2003-04 fishing season. *New Zealand Fisheries Assessment Report 2006/10*. 26 p.

Contreras, A.M.; Marsden, I.D.; Munro, M.H.G. (2012a). Effects of short-term exposure to paralytic shellfish toxins on clearance rates and toxin uptake in five species of New Zealand bivalve. *Marine and Freshwater Research 63*: 166–174.

Contreras, A.M.; Marsden, I.D.; Munro, M.H.G. (2012b). Physiological effects and biotransformation of PSP toxins in the New Zealand scallop, *Pecten novaezelandiae*. *Journal of Shellfish Research 31*: 1151–1159.

Dare, P.J.; Bannister, R.C.A. (1987). Settlement of scallop, *Pecten maximus*, spat on natural substrates off south west England: the hydroid connection. Presentation to the 6th International Pectinid Workshop, Menai Bridge, Wales.

Dare, P.J.; Darby, C.D.; Durance, J.A.; Palmer, D.W. (1994). The distribution of scallops, *Pecten maximus*, in the English Channel and Celtic Sea in relation to hydrographic and substrate features affecting larval dispersal and settlement. *In*: Bourne, N.F.; Bunting, B.L.; Townsend,

L.D. (eds.) *Proceedings of the 9th International Pectinid Workshop, Nanaimo, BC, Canada, April 22-27 1993. Canadian Technical Report of Fisheries and Aquatic Sciences 1994(1)*, pp. 20–27.

Dickie, L.M.; Medcof, J.C. (1963). Causes of mass mortalities of scallops (*Placopecten magellanicus*) in the South-western Gulf of St. Lawrence. *Journal of the Fisheries Research Board of Canada 20*: 451–482.

Dredge, M.C.L.; Marsden, I.D.; Williams, J.R. (2016). Scallop Fisheries, Mariculture and Enhancement in Australasia. *In*: Shumway, S.E.; Parsons, G.J. (eds.) *Scallops: Biology, Ecology, Aquaculture, and Fisheries*, pp. 1127–1170. *Developments in Aquaculture and Fisheries Science, Volume 40*. Elsevier Science, Amsterdam, Holland.

Eckman, J.E. (1987). The role of hydrodynamics in recruitment, growth, and survival of Argopecten irradians (L.) and Anomia simplex (D'Orbigny) within eelgrass meadows. *Journal of Experimental Marine Biology and Ecology 106*: 165–191.

Eckman, J.E.; Peterson, C.H.; Cahalan, J.A. (1989). Effects of flow speed, turbulence, and orientation on growth of juvenile bay scallops *Argopecten irradians concentricus* (Say). *Journal of Experimental Marine Biology and Ecology 132*: 123–140.

Fisheries New Zealand. (2022). Fisheries Assessment Plenary, November 2022: stock assessments and stock status. *Compiled by the Fisheries Science Team, Fisheries New Zealand, Wellington, New Zealand.* 684 p.

Frenette, B.; Parsons, G.J. (2001). Salinity-temperature tolerance of juvenile giant scallops, *Placopecten magellanicus*. Aquaculture Association of Canada Special Publication No. 4. 76–78 p.

Gillespie, P.A.; Maxwell, P.D.; Rhodes, L.L. (2000). Microphytobenthic communities of subtidal locations in New Zealand: Taxonomy, biomass, production, and food-web implications. *New Zealand Journal of Marine and Freshwater Research 34*: 41–53.

Greenfield, B.L.; McCartain, L.D.; Hewitt, J.E. (2019). Manukau Harbour intertidal ecology monitoring 1987 to February 2018. Prepared by NIWA for Auckland Council. Auckland Council technical report, TR2019/025. 68 p.

Gutsell, J.S. (1931). Natural history of the bay scallop (*Pecten irradians*): reproduction and development. *Bulletin of the Bureau of Fisheries 46*: 599–632.

Hale, R.; Godbold, J.A.; Sciberras, M.; Dwight, J.; Wood, C.; Hiddink, J.G.; Solan, M. (2017). Mediation of macronutrients and carbon by post-disturbance shelf sea sediment communities. *Biogeochemistry 135*: 121–133.

Hale, R.; Lam-Gordillo, O.; Lohrer, D.; Williams, J.R.; Handley, S.; Olmedo-Rojas, P.; Middleton, I. (2024). Cumulative effects of stressors on scallops and scallop habitats in the Marlborough Sounds: With insights from sites in Northland, Hauraki Gulf, and eastern Coromandel Peninsula. *New Zealand Aquatic Environment and Biodiversity Report No. 337*. 109 p.

Handley, S.J.; Swales, A.; Horrocks, M.; Gibbs, M.; Carter, M.; Ovenden, R.; Stead, J. (2020). Historic and contemporary anthropogenic effects on granulometry and species composition detected from sediment cores and death assemblages, Nelson Bays, Aotearoa-New Zealand. *Continental Shelf Research 202*: 104147.

Handley, S.J.; Willis, T.J.; Cole, R.G.; Bradley, A.; Cairney, D.J.; Brown, S.N.; Carter, M.E. (2014). The importance of benchmarking habitat structure and composition for understanding the extent of fishing impacts in soft sediment ecosystems. *Journal of Sea Research 86*: 58–68.

Hart, D.R.; Jacobson, L.R.; Tang, J. (2013). To split or not to split: assessment of Georges Bank sea scallops in the presence of marine protected areas. *Fisheries Research 144*: 74–83.

Hart, D.R.; Shank, B.V. (2011). Mortality of sea scallops *Placopecten magellanicus* in the Mid-Atlantic Bight. Comment on Stokesbury et al. (2011). *Marine Ecology Progress Series 443*: 293–297.

Harvey, M.; Bourget, E.; Ingram, G. (1994). The influence of substratum heterogeneity on the settlement of marine bivalve larvae: active versus passive microhabitat selection processes. Presentation to the 9th International Pectinid Workshop, Nanaimo, BC, Canada.

Hatcher, B.G.; Scheibling, R.E.; Barbeau, M.A.; Hennigar, A.W.; Taylor, L.H.; Windust, A.J. (1996). Dispersion and mortality of a population of sea scallop (*Placopecten magellanicus*) seeded in a tidal channel. *Canadian Journal of Fisheries and Aquatic Sciences 53*: 38–54.

Heilmayer, O.; Brey, T.; Portner, H.O. (2004). Growth efficiency and temperature in scallops: a comparative analysis of species adapted to different temperatures. *Functional Ecology 18*: 641–647.

Hine, P.M.; Diggles, B.K. (2002). Prokaryote infections in the New Zealand scallops *Pecten novaezelandiae* and *Chlamys delicatula*. *Diseases of Aquatic Organisms 50*: 137–144.

Hine, P.M.; Wesney, B. (1997). Virus-like particles associated with cytopathology in the digestive gland epithelium of scallops *Pecten novaezelandiae* and toheroa *Paphies ventricosum*. *Diseases of Aquatic Organisms 29*: 197–204.

Honeywill, C.; Paterson, D.; Hagerthey, S. (2002). Determination of microphytobenthic biomass using pulse-amplitude modulated minimum fluorescence. *European Journal of Phycology 37*: 485–492.

Howarth, L.M.; Wood, H.L.; Turner, A.P.; Beukers-Stewart, B. (2011). Complex habitat boosts scallop recruitment in a fully protected marine reserve. *Marine Biology 158*: 1767–1780.

Irlandi, E.A.; Orlando, B.A.; Ambrose, W.G. (1999). Influence of seagrass habitat patch size on growth and survival of juvenile bay scallops, *Argopecten irradians concentricus* (Say). *Journal of Experimental Marine Biology and Ecology 235*: 21–43.

Jesus, B.; Perkins, R.G.; Mendes, C.R.; Brotas, V.; Paterson, D.M. (2006). Chlorophyll fluorescence as a proxy for microphytobenthic biomass: alternatives to the current methodology. *Marine Biology 150*: 17–28.

Kaiser, M.J.; Clarke, K.R.; Hinz, H.; Austen, M.C.V.; Somerfield, P.J.; Karakassis, I. (2006). Global analysis of response and recovery of benthic biota to fishing. *Marine Ecology Progress Series 311*: 1–14.

Kirby-Smith, W.W. (1972). Growth of the bay scallop: The influence of experimental water currents. *Journal of Experimental Marine Biology and Ecology 8*: 7–18.

Langlois, T.J.; Fitzpatrick, B.R.; Fairclough, D.V.; Wakefield, C.B.; Hesp, S.A.; McLean, D.L.; Harvey, E.S.; Meeuwig, J.J. (2012). Similarities between line fishing and baited stereo-video estimations of length-frequency: novel application of Kernel Density Estimates. *PloS One 7*: e45973–e45973.

Legendre, L. (1990). The significance of microalgal blooms for fisheries and for the export of particulate organic carbon in oceans. *Journal of Plankton Research 12*: 681–699.

Lehane, C.; Davenport, J. (2002). Ingestion of mesozooplankton by three species of bivalve: *Mytilus edulis*, *Cerastoderma edule* and *Aequipecten opercularis*. *Journal of the Marine Biological Association of the United Kingdom 82*: 615–619.

Lucas, T.; Palmer, P.; Wang, S.; Scoones, R.; O'Brien, E. (2005). Marking scallops for release and recapture. 83 p. (https://www.frdc.com.au/sites/default/files/products/2005-016-DLD.PDF).

Macdonald, B.; Bricelj, M.; Shumway, S. (2006). Physiology: Energy Aquisition and Utilisation. *In*: Shumway, S.E.; Parsons, G.J. (eds.) *Scallops: Biology, Ecology and Aquaculture*, pp. 417–492. Elsevier, Amsterdam.

MacDonald, B.A.; Thompson, R.J. (1985a). Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. 1. Growth rates of shell and somatic tissue. *Marine Ecology Progress Series 25*: 279–294.

MacDonald, B.A.; Thompson, R.J. (1985b). Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. 2. Reproductive output and total production. *Marine Ecology Progress Series 25*: 295–303.

MacDonald, B.A.; Thompson, R.J. (1986a). Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. 3. Physiological ecology, the gametogenic cycle and scope for growth. *Marine Biology 93*: 37–48.

MacDonald, B.A.; Thompson, R.J. (1986b). Production, dynamics and energy partitioning in two populations of the giant scallop *Placopecten magellanicus* (Gmelin). *Journal of Experimental Marine Biology and Ecology 101*: 285–299.

MacDonald, B.A.; Thompson, R.J.; Bayne, B.L. (1987). Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. 4. Reproductive effort, value and cost. *Oecologia 72*: 550–556.

MacGibbon, D.J. (2019). Inshore trawl survey of the west coast South Island and Tasman and Golden Bays, March-April 2019 (KAH1902). *New Zealand Fisheries Assessment Report 2019/64*: 87 p.

Mason, J. (1983). Scallop and Queen Fisheries in the British Isles. Fishing News Books Ltd (Buckland Foundation), Farnham, UK. 144 p.

Maxwell, K.; Johnson, G.N. (2000). Chlorophyll fluorescence — a practical guide. *Journal of Experimental Botany 51*: 659–668.

Mendo, T.; Lyle, J.M.; Moltschaniwskyj, N.A.; Tracey, S.R.; Semmens, J.M. (2014). Habitat characteristics predicting distribution and abundance patterns of scallops in D'Entrecasteaux Channel, Tasmania. *PLoS ONE 9*: e85895.

Mercaldo, R.S.; Rhodes, E.W. (1982). Influence of reduced salinity on the Atlantic bay scallop *Argopecten irradians* (Lamarck) at various temperatures. *Journal of Shellfish Research 2*: 177–181.

Michael, K.P.; Handley, S.; Williams, J.R.; Tuck, I.D.; Gillespie, P.A.; Cornelisen, C.; Basher, L.; Chang, F.H.; Brown, S.N.; Zeldis, J. (2015). A summary of information and expert opinion to help rebuild shellfish fisheries in Golden and Tasman Bays. NIWA Information Series No. 84. 112 p.

Miller, G.C.; Allen, D.M.; Costello, T.J. (1981). Spawning of the calico scallop *Argopecten gibbus* in relation to season and temperature. *Journal of Shellfish Research 1*: 17–21.

Miller, G.C.; Richards, W.J. (1980). Reef fish habitat, faunal assemblages and factors determining distributions in the south Atlantic Bight. *Proceedings of the Gulf and Caribbean Fisheries Institute 32*: 114–130.

Ministry for Primary Industries (2013). Aquatic Environment and Biodiversity Annual Review 2013, Compiled by the Fisheries Management Science Team, Ministry for Primary Industries. Wellington, New Zealand. 538 p.

Morrison, M. (1999). Population dynamics of scallops, *Pecten novaezelandiae*, in the Hauraki Gulf. Unpublished PhD thesis. University of Auckland, Auckland, New Zealand. 157 p.

Morton, B. (1996). The biology and functional morphology of *Minnivola pyxidatus* (Bivalvia: Pectinoidea). *Journal of Zoology 240*: 735–760.

Moss, G.; Williams, J.R.; Beaumont, J.; Cummings, V.; Barr, N.; Calle, A.; Mobilia, V.; Halliday, J. (2023). Effects of elevated suspended sediment concentrations on juvenile scallops (*Pecten novaezelandiae*). NIWA Internal Report 2022305AK. Unpublished report held by NIWA Auckland, New Zealand. 32 p.

Nelson, J.R.; Eckman, J.E.; Robertson, C.Y.; Marinelli, R.L.; Jahnke, R.A. (1999). Benthic microalgal biomass and irradiance at the sea floor on the continental shelf of the South Atlantic Bight: Spatial and temporal variability and storm effects. *Continental Shelf Research 19*: 477–505.

Nesbit, G.J. (1999). Reseeding and hatchery potential of *Pecten novaezelandiae* and effects of recreational harvesting. Unpublished MSc thesis. University of Auckland, Auckland, New Zealand. 145 p.

Nicholls, P.; Hewitt, J.E.; Halliday, J. (2003). Effects of suspended sediment concentrations on suspension and deposit feeding marine macrofauna. Auckland Regional Council Technical Publication 211. 32 p.

Nicholson, J. (1978). Feeding and reproduction in the New Zealand scallop *Pecten novaezelandiae*. Unpublished MSc thesis. University of Auckland, New Zealand. 75 p.

O'Connor, W.A.; Heasman, M.P. (1998). Ontogenetic changes in salinity and temperature tolerance in the doughboy scallop, *Mimachlamys asperrima*. *Journal of Shellfish Research 17*: 89–95.

Orensanz, J.M.; Parma, A.M.; Smith, S.J. (2016). Dynamics, Assessment and Management of Exploited Natural Populations. *In*: Shumway, S.E.; Parsons, G.J. (eds.) *Scallops: Biology, Ecology and Aquaculture*, pp. 611–695. Elsevier, Amsterdam, Holland.

Paul, J.D. (1980). Salinity–temperature relationships in the queen scallop *Chlamys opercularis*. *Marine Biology 56*: 295–300.

Paul, J.D. (1981). Nautral settlement and early growth of spat of the Queen Scallop *Chlamys opercularis* (L.), with reference to formation of the first growth ring. *Journal of Molluscan Studies 47*: 53–58.

Peake, B.M.; Marsden, I.D.; Ashoka, S.; Bremner, G. (2010). Interspecific and geographical variation in trace metal concentrations of New Zealand scallops. *Journal of Shellfish Research 29*: 387–394.
Pilditch, C.A.; Emerson, C.W.; Grant, J. (1997). Effect of scallop shells and sediment grain size on phytoplankton flux to the bed. *Continental Shelf Research 17*: 1869–1885.
Pilditch, C.A.; Grant, J. (1999). Effect of variations in flow velocity and phytoplankton concentration on sea scallop (*Placopecten magellanicus*) grazing rates. *Journal of Experimental Marine Biology and Ecology 240*: 111–136.
Pommer, C.D.; Olesen, M.; Hansen, J.L.S. (2016). Impact and distribution of bottom trawl fishing on mud-bottom communities in the Kattegat. *Marine Ecology Progress Series 548*: 47–60.
Porri, F.; Jordaan, T.; McQuaid, C.D. (2008). Does cannibalism of larvae by adults affect settlement and connectivity of mussel populations? *Estuarine, Coastal and Shelf Science 79*: 687–693.
Powers, S.P.; Kittinger, J.N. (2002). Hydrodynamic mediation of predator-prey interactions: differential patterns of prey susceptibility and predator success explained by variation in water flow. *Journal of Experimental Marine Biology and Ecology 273*: 171–187.
Prentice, I.C.; Farquhar, G.D.; Fasham, M.J.R.; Goulden, M.L.; Heimann, M.; Jaramillo, V.J.; Kheshgi, H.S.; Le Quéré, C.; Scholes, R.J.; Wallace, D.W.R.; et. al. (2001). The carbon cycle and atmospheric carbon dioxide. *In*: *Climate change 2001: the scientific basis, Intergovernmental panel on climate change, 2001.* , pp. 183–237.
Rijnsdorp, A.D.; Bolam, S.G.; Garcia, C.; Hiddink, J.G.; Hintzen, N.T.; van Denderen, P.D.; van Kooten, T. (2018). Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. *Ecological Applications 28*: 1302–1312.
Schick, D.F.; Shumway, S.E.; Hunter, M.A. (1988). A comparison of growth rate between shallow water and deep water populations of scallops, *Placopecten magellanicus* (Gmelin, 1791), in the Gulf of Maine. *American Malacological Bulletin 6*: 1–8.
Serb, J.M. (2016). Reconciling Morphological and MolecularApproaches in Developing a Phylogeny for the Pectinidae (Mollusca: Bivalvia). *In*: Shumway, S.E.; Parsons, G.J. (eds.) *Scallops: Biology, Ecology and Aquaculture*, pp. 1–29. Elsevier, Amsterdam, Holland.
Shank, B.V.; Hart, D.R.; Friedland, K.D. (2012). Post-settlement predation by sea stars and crabs on the sea scallop in the Mid-Atlantic Bight. *Marine Ecology Progess Series 468*: 161–177.
Shumway, S.E.; Parsons, G.J. (eds.) (2016). *Scallops: Biology, Ecology, Aquaculture and Fisheries*. Elsevier, Amsterdam, Holland. 1196 p.
Smith, P.; Diggles, B. (1999). Coromandel shellfish update, November 1999. Unpublished NIWA Wellington report. 2 p.
Southern Scallop Working Group & Fisheries New Zealand. (2020). Southern Scallop Strategy: Marlborough Sounds. *New Zealand Government publication.* https://www.fisheries.govt.nz/news-and-resources/consultations/draft-marlborough-sounds-scallop-strategy/?utm_source=notification-email: 13 p.
Spires, J.E.; North, E.W. (2022). Marking the shells of juvenile and adult eastern oysters, *Crassostrea virginica*, with the fluorochrome dye calcein and measuring growth and mortality after marking. *Journal of Molluscan Studies 88*: eyac004.
Stevens, P.M. (1987). Response of excised gill tissue from the New Zealand scallop *Pecten novaezelandiae* to suspended silt. *New Zealand Journal of Marine and Freshwater Research 21*: 605–614.
Stockton, W.L. (1984). The biology and ecology of the epifaunal scallop *Adamussium colbecki* on the west side of McMurdo Sound, Antarctica. *Marine Biology 78*: 171–178.
Stokesbury, K.D.E.; Himmelman, J.H. (1993). Spatial distribution of the giant scallop *Placopecten magellanicus* in unharvested beds in the Baie des Chaleurs, Que´bec. *Marine Ecology Progess Series 96*: 159–168.
Stokesbury, K.D.E.; Himmelman, J.H. (1995). Biological and physical variables associated with aggregations of the giant scallop *Placopecten magellanicus*. *Canadian Journal of Fisheries and Aquatic Sciences 52*: 743–753.
Suresh, M.; Arularasan, S.; Nithyanandan, M. (2013). Occurrence of Tranquebar scallop *Volachlamys tranquebaria* in Vellar estuary, south-east coast of India. *Marine Biodiversity Records 6*: e38.

Talman, S.G.; Norkko, A.; Thrush, S.F.; Hewitt, J.E. (2004). Habitat structure and the survival of juvenile scallops *Pecten novaezelandiae*: comparing predation in habitats with varying complexity. *Marine Ecology Progress Series 269*: 197–207.

Taylor, R.B.; Morrison, M.A. (2008). Soft-sediment habitats and fauna of Omaha Bay, northeastern New Zealand. *Journal of the Royal Society of New Zealand 38*: 187–214.

Thouzeau, G.; Robert, G.; Smith, S.J. (1991). Spatial variability in distribution and growth of juvenile and adult sea scallops *Placopecten magellanicus* (Gmelin) on eastern Georges Bank (Northwest Atlantic). *Marine Ecology Progess Series 74*: 205–218.

Thrush, S.F.; Hewitt, J.E.; Cummings, V.J.; Dayton, P.K. (1995). The impact of habitat disturbance by scallop dredging on marine benthic communities: what can be predicted from the results of experiments? *Marine Ecology Progress Series 129*: 141–150.

Thrush, S.F.; Hewitt, J.E.; Hickey, C.W.; Kelly, S. (2008). Multiple stressor effects identified from species abundance distributions: interactions between urban contaminants and species habitat relationships. *Journal of Experimental Marine Biology and Ecology 366*: 160–168.

Twist, B.A.; Hepburn, C.D.; Rayment, W.J. (2015). Distribution of the New Zealand scallop (*Pecten novaezealandiae*) within and surrounding a customary fisheries area. *ICES Journal of Marine Science 73*: 384–393.

Twist, B.A.; Rayment, W.J.; Hepburn, C.D. (2016). Movement patterns of adult scallops (*Pecten novaezealandiae*) within a customary fisheries reserve: Implications for fine scale spatial management. *Fisheries Research 174*: 160–166.

Uribe, E.; Blanco, J.L.; Yamashiro, C. (2003). Effect of salinity on the distribution of *Argopecten purpuratus* on the SW Pacific coast. *In*: *Book of Abstracts, 14th International Pectinid Workshop, St. Petersburg, FL, 23-29 April 2003*, pp. 125–126.

Ursin, E. (1956). Distribution and growth of the queen, *Chlamys opercularis* (Lamellibranchiata) in Danish and Faroese waters. *Meddelelser fra Danmarks Fiskeri-og Havundersøgelser Ny Serie 1*: 1–31.

Vahl, O. (1980). Seasonal variatins in seston and in the growth rate of the iceland scallop, *Chlamys islandica* (O.F. Müller) from balsfjord, 70°N. *Journal of Experimental Marine Biology and Ecology 48*: 195–204.

Valiela, I.; Foreman, K.; LaMontagne, M.; Hersh, D.; Costa, J.; Peckol, P.; DeMeo-Andreson, B.; D'Avanzo, C.; Babione, M.; Sham, C.-H.; Brawley, J.; Lajtha, K. (1992). Couplings of watersheds and coastal waters: Sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. *Estuaries 15*: 443–457.

Ventilla, R.F. (1982). The scallop industry in Japan. *Advances in Marine Biology 20*: 310–390.

Wallace, J.C.; Reinsnes, T.G. (1985). The significance of various environmental parameters for growth of the Iceland scallop, *Chlamys islandica* (Pectinidae), in hanging culture. *Aquaculture 44*: 229–242.

Webb, S. (2018). Health assessment of scallops (*Pecten novaezelandiae*) from CSEC farm in Tasman Bay. Unpublished report prepared by Cawthron Institute for Fisheries New Zealand. 7 p.

Wei, T.; Simko, V. (2021). R package 'corrplot': Visualization of a Correlation Matrix. (Version 0.92).

Wildish, D.J.; Kristmanson, D.D. (1988). Growth response of giant scallops to periodicity of flow. *Marine Ecology Progress Series 42*: 163–169.

Wildish, D.J.; Kristmanson, D.D.; Hoar, R.L.; DeCoste, A.M.; McCormick, S.D.; White, A.W. (1987). Giant scallop feeding and growth responses to flow. *Journal of Experimental Marine Biology and Ecology 113*: 207–220.

Wildish, D.J.; Saulnier, A.M. (1992). The effect of velocity and flow direction on the growth of juvenile and adult giant scallops. *Journal of Experimental Marine Biology and Ecology 155*: 133–143.

Wildish, D.J.; Saulnier, A.M. (1993). Hydrodynamic control of filtration in *Placopecten magellanicus*. *Journal of Experimental Marine Biology and Ecology 174*: 65–82.

Willan, R.C. (1981). Soft-bottom assemblages of Paterson Inlet, Stewart Island. *New Zealand Journal of Zoology 8*: 229–248.

Williams, J.; Bian, R.; Olsen, L.; Stead, J. (2021). Survey of scallops in SCA 7, May 2020. *New Zealand Fisheries Assessment Report 2021/09*: 54 p.

Williams, J.R.; Babcock, R.C. (2004). Patterns of reproduction and spawning behaviour for scallops *Pecten novaezelandiae* in northeastern New Zealand. Presentation to the Journal of Shellfish

Research, April, Abstracts of Technical Papers Presented at the 96th Annual Meeting of the National Shell Fisheries Association, March 1-5, 2004, Honolulu, Hawaii, USA.

Williams, J.R.; Babcock, R.C. (2005). Assessment of size at maturity and gonad index methods for the scallop *Pecten novaezelandiae*. *New Zealand Journal of Marine and Freshwater Research 39*: 851–864.

Williams, J.R.; Bian, R.; Carter, M.; Evans, O.; Hughes, R.; Jordan, L.; Middleton, C.; Olsen, L.; Stead, J. (2024a). Dive and dredge surveys of scallops in SCA 7, 2021. New Zealand Fisheries Assessment Report 2024/57. 51 p.

Williams, J.R.; Bian, R.; Middleton, C.M.; Hughes, R.; Evans, O.; Buckthought, D.; Parkinson, D.; Taylor, R. (2024b). Dive and dredge surveys of scallops in SCA 1 and SCA CS, 2021. *New Zealand Fisheries Assessment Report 2024/36*. 64 p.

Williams, J.R.; Bian, R.; Olsen, L.; Stead, J.; Tuck, I. (2019). Dredge survey of scallops in Marlborough Sounds, May 2019. *New Zealand Fisheries Assessment Report 2019/69*. 50 p.

Williams, J.R.; Hartill, B.; Bian, R.; Williams, C.L. (2014). Review of the Southern scallop fishery (SCA 7). *New Zealand Fisheries Assessment Report 2014/07*. 71 p.

Williams, J.R.; Parkinson, D.M.; MacGibbon, D.J.; Olsen, L.; Roberts, C.L. (2015). SCA 7 stock survey, November 2015. *New Zealand Fisheries Assessment Report 2015/79*. 44 p.

Woodin, S.A. (1976). Adult-larval interactions in dense infaunal assemblages: patterns of abundance. *Journal of Marine Research 34*: 25–41.

Woods, C.M.C.; Hayden, B.J. (1998). An observation of the *Turbellarian Paravortex* sp. in the New Zealand scallop *Pecten novaezelandiae* (Bivalvia: Pectinidae). *New Zealand Journal of Marine and Freshwater Research 32*: 551–553.

Yamamoto, G. (1956). On the behaviour of the scallop under some environmental conditions with special reference to effects of suspended silt, lack of soluble oxygen and others on ciliary movement of gill pieces. *Japanese Journal of Ecology 5*: 172–175.

Yamamoto, G. (1960). Mortalities of the scallop during its life cycle. *Bulletin of Marine Biological Station, Asamushi, Tohoku University 10*: 149–152.

Yang, B.; Gao, X.; Zhao, J.; Liu, Y.; Xie, L.; Lv, X.; Xing, Q. (2021). Potential linkage between sedimentary oxygen consumption and benthic flux of biogenic elements in a coastal scallop farming area, North Yellow Sea. *Chemosphere 273*: 129641.

Young, P.C.; Martin, R.B. (1989). The scallop fisheries of Australia and their management. *CRC Critical Reviews in Aquatic Sciences 1*: 615–638.

Young, P.C.; Martin, R.B.; McLoughlin, R.J.; West, G. (1989). Variability in spatfall and recruitment of commercial scallops (*Pecten fumatus*) in Bass Strait. Presentation to the Australasian Scallop Workshop, Hobart, Australia.

Zuur, A.F.; Ieno, E.N.; Walker, N.; Saveliev, A.A.; Smith, G.M. (2009). Mixed Effects Models and Extensions in Ecology with R. *Statistics for Biology and Health.* Springer, New York, NY. 574 p.

9. APPENDIX 1

Scallop histopathology investigation by MPI

Scallops collected in December 2018 and retained for disease analysis by the MPI Animal Health Laboratory (AHL), Wellington were split into two size groups (< 80 mm and ≥ 80 mm). The number of scallops available for examination per site varied (Table).

Table A1.1: Numbers of scallops analysed for disease by size group at each site, December 2018.

Site	Scallop length	
	< 80 mm	≥ 80 mm
Awaroa	4	0
Bark	10	4
Croisilles	9	8
Croisilles 2	11	3
Farewell	7	8
Motueka	1	0
Parapara	1	0
Patons	3	0
Puponga	4	0
Wainui	10	8
Total	60	31

General comments from the MPI Animal Health Laboratory (report received 19 March 2020):

"Unfortunately, the majority of shellfish examined were autolysed, with cell detail lost in especially the digestive gland and gills. Adequate evaluation and interpretation of the gills was not possible.

The accumulation of pigment material within digestive gland epithelium is likely to be associated with digestive functions and accumulation and storage of chlorophyll breakdown products and formation of a phaeopigment within lipid storage vesicles.

Scattered small numbers of haemocyte infiltrates are often seen within the digestive gland stroma and these may be within normal limits. However, with larger aggregates and higher numbers of cells, these could indicate an inflammatory response to either ingested material or infectious/parasitic organisms moving through the tissue and digestive gland. A clear cause for some of the heavier cellular infiltrates was not apparent in the sections examined.

The exact nature of the organisms seen within the lumen of the digestive tract is uncertain. However, the structures are suggestive of an 'egg' stage with development into some different life stages within the digestive tract. The organisms are not associated with any clear pathology and are likely to have been ingested during normal feeding. The organisms are present to variable degrees in the scallops with a few have high numbers in the lumen suggesting higher numbers of these organisms in the local water column and environment. They are not thought to be parasitizing the scallops.

The female gonads of a large proportion of the scallops showed mixed sizing of the oocytes with variable increases in cellular infiltrates and fibrous stroma. This is most likely associated with spawning and post spawning changes in the gonad.

Rickettsia-like organisms (RLOs) were observed in scallops from the Croisilles 2 and Farewell sites. Inflammation was not associated with the presence of these RLOs and their significance is uncertain."

The MPI Animal Health Laboratory report also contained specific comments on each individual scallop number (AHL number) screened. The information contained within these specific comments was used to derive categorical data in terms of either the presence/absence or the numerical level of severity for the various histopathological features observed. Boxplots were used to assess the level of severity of the different measures by site for scallops less than 80 mm length (for consistency across sites), although inclusion of larger scallops (where available) did not change the overall patterns. There were significant between-site differences (ANOVA, poisson error structure) for the severity of pigment accumulation, organisms in the digestive tract and glands, and haemocyte infiltrates, although no consistent patterns were evident (Figure).

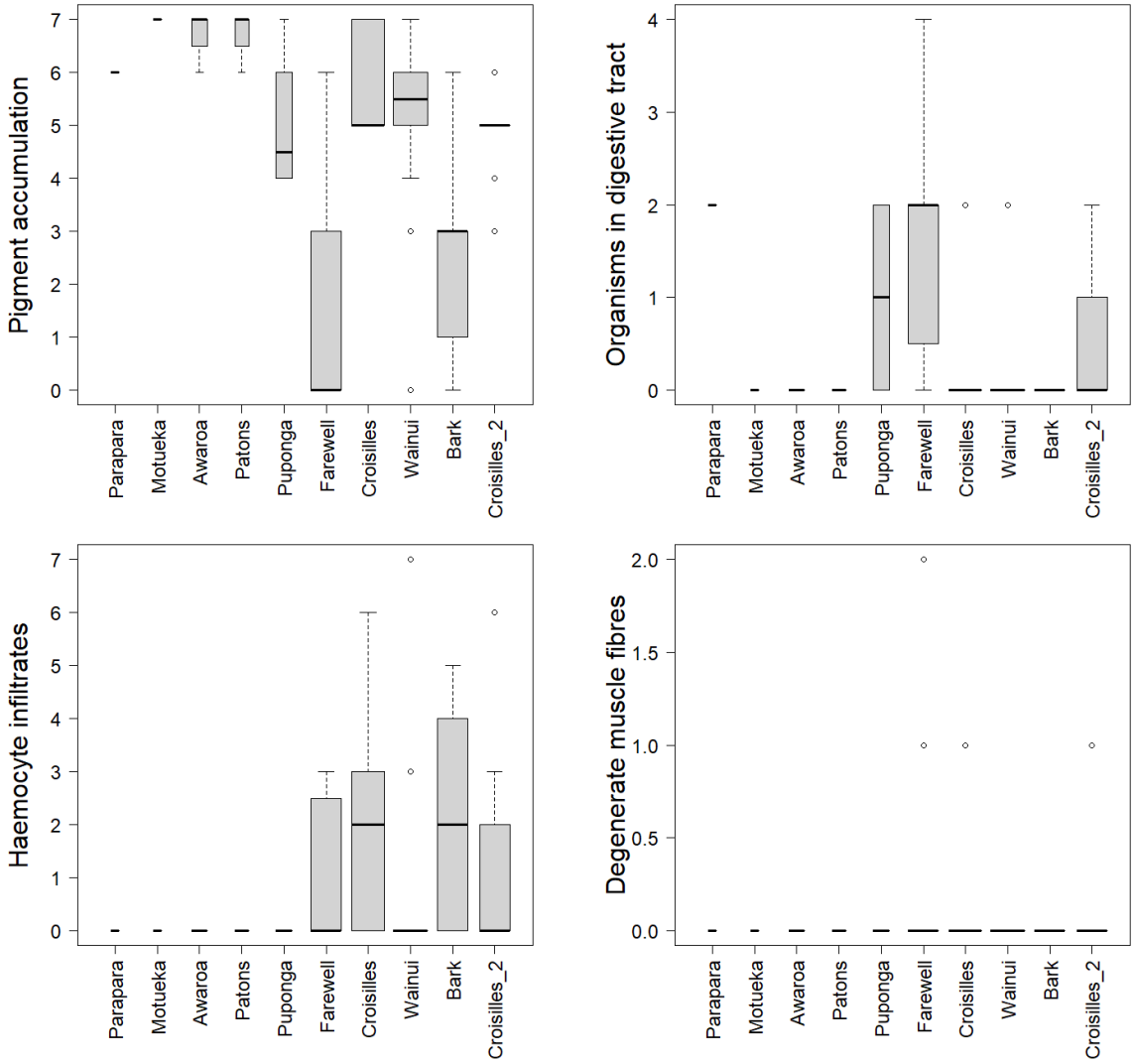

Figure A1.1: Boxplots of histological features found in scallops collected in December 2018, by site. Top left: level of severity of pigment accumulation; top right: level of severity of organisms in the digestive tract and glands; bottom left: levels of severity of haemocyte infiltrates; bottom right: level of severity of degenerate muscle fibres. Sites are ordered from left to right with increasing scallop density (scallops < 80 mm m^{-2} in December 2018) (see Table 5).