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Expansion of shellfish aquaculture has no impact on settlement rates

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ABSTRACT: Wild shellfish reefs have been decimated in many parts of the world over the last century, diminishing their vital ecological roles as habitat generators and the ecosystem services they provide, such as water filtration. Over this same timescale, shellfish aquaculture has rapidly expanded to become an impressive global industry with an annual worldwide production worth US$35.4 billion in 2020. Both wild reefs and aquaculture operations typically rely on abundant shellfish settlement levels to maintain their respective populations. At the same time, shellfish aquaculture has the potential to influence settlement, as the addition of cultured shellfish to an ecosystem increases the quantity of reproductive adults and may therefore increase settlement rates. Alternatively, shellfish aquaculture may lead to an overall reduction in settlement in an ecosystem, either directly through cannibalistic consumption of larvae or indirectly by straining carrying capacity. We assessed the role of marine shellfish aquaculture on settlement by comparing changes in the abundance of settling green-lipped mussels *Perna canaliculus* with the expansion of mussel farms at the north end of New Zealand's South Island over a 47 yr timespan. Overall, mussel settlement did not increase over this period despite an estimated 16 000-fold increase in the number of mussels living in the region as mussel aquaculture proliferated. The disconnect between the extent of mussel settlement and mussel aquaculture was consistent across 3 separate areas within the region, suggesting that aquaculture mussels may be unable to produce larvae capable of settlement and emphasizing the importance of wild mussel populations for ecosystem resilience.

KEY WORDS: Larval settlement · Green-lipped mussels · *Perna canaliculus* · Spat · New Zealand

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1. INTRODUCTION

Shellfish reefs, like those created by oysters and mussels, have been decimated globally as a result of overharvesting and habitat loss (Lotze et al. 2006, Beck et al. 2009). The destruction of these reefs has resulted in the loss of the complex habitats they create (Suchanek 1985) and the valuable ecosystem services they provide, such as water filtration (Bayne 1976), wave attenuation (Wiberg et al. 2019), sediment stabilization (Meadows et al. 1998), and denitrification (Hillman et al. 2021, Sea et al. 2021). Natural recovery of shellfish reefs has been slow, even in areas that are no longer subject to harvesting (Beck et al. 2011, Zu Ermgassen et al. 2012). This recovery is typically reliant on larval supply and settlement from remnant populations, as most reef-forming shellfish are broadcast spawners with impressive larval dispersal kernels (Bayne 1976, Hofmann et al. 1992). When this larval supply or settlement is limited or non-existent, wild shellfish reefs cannot recover (Marshall et al. 2020) and are instead reliant on restoration efforts to transplant populations in an effort to restore a sufficient supply of larval settlers

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for the wild population to recover (e.g. Schulte et al. 2009, Wilcox et al. 2020, Alder et al. 2021).

In addition to wild populations, reef-building shellfish are also common aquaculture species, representing over half of the global animal aquaculture production by total volume (FAO 2020). Aquaculture production of molluscs, primarily bivalves, reached 17.7 million t worldwide in 2020, with an estimated value of US$35.4 billion (FAO 2020). Shellfish farms typically suspend oysters or mussels on lines in the water column or in baskets near the surface rather than being placed directly on shorelines or the seafloor like wild reefs (Wijsman et al. 2018). Nevertheless, these farmed populations are also often reliant on wild settlement, as seed-stock is commonly collected from settled shellfish attached to either natural substrata (e.g. Buchanan & Babcock 1997, Alfaro & Jeffs 2002) or from artificial settlement surfaces deployed in the water column (e.g. Camacho et al. 1995, Forrest & Creese 2006, Skelton & Jeffs 2020). While some aquaculture producers have shifted to seed generated from hatchery-reared larvae (Nascimento-Schulze et al. 2021), this wild supply is still a vital part of the industry in many places. For example, over 90% of the seed used in the ~100000 t yr^{-1} production from the green-lipped mussel *Perna canaliculus* aquaculture industry in New Zealand comes from harvested wild mussel seed (Jeffs et al. 1999, South et al. 2020).

While much of the shellfish aquaculture industry relies on wild mussel settlement, it also has the potential to impact this same supply, as cultured mussels may produce or consume enough larvae to influence local settlement levels (Norrie et al. 2020, Ridlon et al. 2021). However, the direction and extent of the influence that aquaculture-based shellfish populations may have on mussel settlement is largely unknown. Larval production from dense aquaculture aggregations is often overlooked in research into benefits of shellfish aquaculture (e.g. Newell 2004, van der Schatte Olivier et al. 2020), despite some modelling demonstrating that enhanced larval subsidies from mussel farms have the potential to increase the settlement rates of local larvae (Norrie et al. 2020). Conversely, shellfish aquaculture may also reduce settlement rates, as farmed shellfish may exhaust the local carrying capacity (Waite et al. 2005, Duarte et al. 2008, Wijsman et al. 2018), hindering the survival of wild settlers. Additionally, some bivalves cannibalize their own larvae (Davenport et al. 2000, Zeldis et al. 2004, Alfaro 2006), which may reduce the available larval stock and therefore settlement rates in an area.

At an ecosystem scale, the role of aquaculture-reared shellfish as possible net producers or consumers of larvae remains unresolved because of the practical difficulties in accounting for the fate of larvae in large and complex ecosystems (Gawarkiewicz et al. 2007, Nolasco et al. 2018). The most common methods of tracking dispersal of small larvae are biophysical models which couple oceanographic data with knowledge on larval behaviour (e.g. Cowen et al. 2000, Werner et al. 2007, Thomas et al. 2016) and natural tagging which tracks micro-chemical fingerprints retained in carbonate structures or genetic markers (e.g. Galindo et al. 2010, Ricardo et al. 2015, Gomes et al. 2016). While these approaches provide invaluable estimates of larval supply, they are often unlinked to direct measures of *in situ* larvae (Gawarkiewicz et al. 2007) and are constrained in their ability to differentiate or quantify larval supply from source populations (e.g. shellfish aquaculture farms versus adjacent wild shellfish reefs). One possible alternative approach is to couple known ecosystem-wide changes with long-term *in situ* settlement monitoring, allowing for direct comparisons between settlement and major changes to an ecosystem like the inception and growth of an aquaculture industry. While this approach is intrinsically correlative, it is grounded in empirical field measurements of larvae and can therefore augment and validate traditional model- or marker-based approaches.

In this study, we aimed to determine the influence of shellfish aquaculture on settlement rates by comparing green-lipped mussel settlement over 4 decades of data across 150 km of the northern end of the South Island of New Zealand with the expansion of mussel aquaculture across the same temporal and spatial scales. Ultimately, we sought to address how marine shellfish aquaculture influences shellfish settlement and provide insights for aquaculture and conservation managers on methods to maintain and enhance settlement rates.

2. MATERIALS AND METHODS

2.1. Study species and region

Green-lipped mussels are endemic to New Zealand and are found in a variety of habitats on hard and soft substrates from the intertidal zone to depths of 50 m (Jeffs et al. 1999). Green-lipped mussels are broadcast spawners and have a pelagic larval duration between 4 and 6 wk. Depending on connectivity and water currents, larvae can travel anywhere from just a few km to hundreds of km over this duration (Gardner et al. 2021). Larval mussels then undergo settlement, typically attaching onto filamentous surfaces like macroalgae before eventually transitioning to adult mussel reefs or other hard surfaces (Buchanan & Babcock 1997, Alfaro & Jeffs 2002, Alfaro et al. 2006).

The northern end of the South Island supports around 70% of New Zealand's NZ$360 million (USD$230 million) mussel farming industry (Stenton-Dozey et al. 2021), which consists of mussels grown in blocks of parallel longlines that culture mussels on ropes suspended in the water column between large surface floats (Jeffs et al. 1999, Dawber 2004). Prior to the inception of mussel aquaculture in the 1970s, this region was also central to a wild mussel harvesting industry, which resulted in the depletion of widespread populations of wild mussels through extensive dredging and handpicking (Urlich & Handley 2020). An extended period without natural recovery of wild populations followed, leaving current mussel populations at less than 3% of historical levels in some areas (T. A. Toone unpubl. data).

This region is comprised of 3 distinct water bodies where wild mussels were historically harvested and subsequently supplanted by mussel aquaculture: Golden Bay, Tasman Bay, and the Marlborough Sounds (Fig. 1). Golden Bay and Tasman Bay are both wide and shallow coastal embayments, while the Marlborough Sounds are a series of drowned river valleys with more narrow openings to Cook Strait and greater freshwater influence (Urlich & Handley 2020).

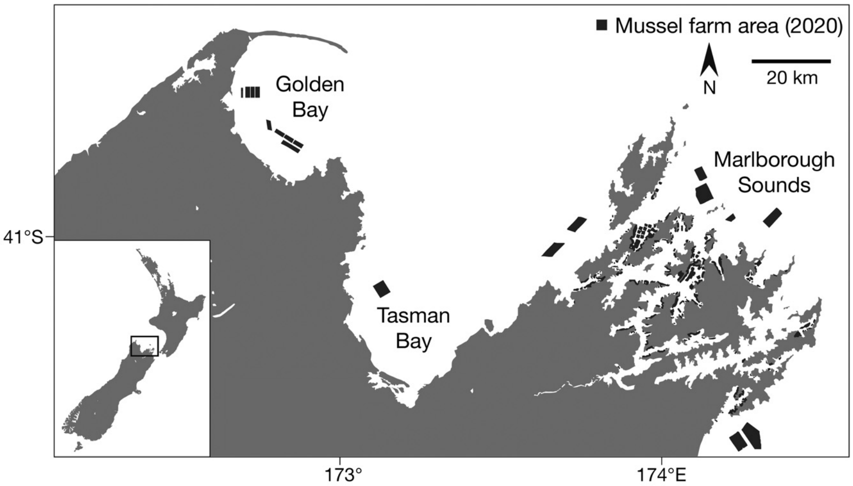

Fig. 1. Study region at the northern end of the South Island of New Zealand. Labels indicate major water bodies analysed for larval supply. Dark grey polygons indicate mussel aquaculture sites with harvesting permits in 2020. Only operationally active farms were included in analyses

2.2. Mussel population abundance and composition

To determine the impact of mussel aquaculture on settlement rates, it was first important to estimate the changes in the total cultured mussel population over time. Cultured mussel populations were estimated using aquaculture harvest data from 2007 to 2020, the extent of the available data from Aquaculture New Zealand. To estimate mussel harvests prior to 2007, the average harvest tonnage per hectare was calculated for 2007–2020 and then combined with the spatial extent of mussel farms per year beginning with the first commercial mussel farms in the area in 1976. While farming densities and methods shifted from 1976 to 2007, this calculation allows for an estimation of commercial harvests prior to comprehensive record keeping. To estimate total cultured mussel populations and allow comparison with wild mussel abundances, these tonnage figures were converted to total number of mussels following the 20 000 mussels t^{-1} approximation commonly used in the industry (Wilcox et al. 2018). The final abundance of cultured mussels per year was calculated by doubling these annual harvesting numbers to account for a 2 yr growing period before mussels are harvested, meaning that the mussels harvested in any given year are only around half of the total farmed mussels in the water that year (Dawber 2004).

As wild mussels are a potential source for settling larvae, we also estimated historic wild mussel populations. Reliable wild harvesting and remnant population data only exist for the Marlborough Sounds, so this analysis excluded Golden Bay and Tasman Bay. Mussels harvested from the wild were quantified during the period of active commercial harvesting from 1960 to 1983 (Paul 2012, Francis & Paul 2013). These figures were converted from sacks of harvested mussels to number of mussels using contemporaneous conversion factors (Stead 1971, Francis & Paul 2013). These conversions are substantially lower than those used for cultured mussels because wild mussels are larger, heavier, and have significant biofouling, which decreases the number of mussels t^{-1} (Stead 1971). To estimate the entire wild population prior to the inception of commercial harvesting, these annual harvests were summed, as any mussels harvested over this period were present in the wild prior to harvest. This number was then increased by 3%, representing the estimated unharvested remnant population in the Marlborough Sounds (T. A. Toone unpublished data). To determine the size of the wild mussel population for the following years, the 1960 total wild population was decreased by the amount harvested in each subsequent year.

The final estimates of mussel population composition from 1960 to 2020 were determined by combining the estimated wild and cultured populations per year. These population estimates likely underestimate both populations, as some wild mussels would have been harvested but unrecorded and some cultured mussels are lost in the harvesting process. However, these methods should provide estimates that are within an order of magnitude of accuracy which allows for comparison if the differences between the 2 populations are extreme.

2.3. Mussel settlement

To quantify *in situ* settlement of mussels for comparison to aquaculture, measurements of green-lipped mussel settlement from 1974 to 2020 were compiled from long-term sampling conducted to determine the timing of commercial catching of seed mussels (data provided by the New Zealand Marine Farming Association). Mussel settlement was monitored by deploying frames with 0.25 m sections of polypropylene rope at sites throughout the study region ranging from 1 to 15 m depth. Once a week, the rope was replaced, and the recovered rope was analysed to count the numbers of recently settled green-lipped mussels, which was then standardized per m of rope. Settlement monitoring began in the Marlborough Sounds from 1974 to 1985, then was paused from 1986 to 1992, and restarted with sites in both the Marlborough Sounds and Golden Bay in 1993. The monitoring programme expanded to include sites in Tasman Bay in 1999. In total, 30 033 sampling ropes were analysed over the 47 yr period. Atalah & Forrest (2019) provided a more detailed description of the mussel settlement monitoring as well as an analysis of the impact of environmental parameters on mussel settlement, which is not discussed here.

While the mussel settlement records in the study areas are temporally and spatially extensive, the settlement sampling sites were originally chosen with industry concerns in mind, and not selected specifically to test the impact of expanding mussel aquaculture on settlement rates. Therefore, these sampling sites are likely to have higher settlement than randomly selected sites. However, the sites do cover a wide gradient from locations that never contained mussel aquaculture at certain sampling timepoints to locations with dozens of nearby mussel farms.

2.4. Mussel aquaculture expansion

The spatial extent of coastal mussel farms over time in the 3 study areas was determined by interrogating the records of government agencies responsible for permitting marine farms from 1976 to 2020 (Tasman and Marlborough District Councils). Permit start dates, expiration dates, locations, and farm spatial coverage were extracted from these records to generate a database for current and historic mussel farms in the study region which could be compared with mussel settlement.

2.5. Analyses

All data analyses were undertaken using RStudio v2022.02.1 (R Core Team 2021). Mean mussel settlement was compared between regions using nonparametric tests, specifically Kruskal-Wallis tests to determine significance and Wilcoxon rank sum tests to calculate pairwise comparisons between study areas. Differences were considered significant at $p < 0.05$. Any long-term trends in settlement in each area were monitored using Spearman correlations to examine the relationship between year and spat settlement.

Additionally, mean green-lipped mussel settlement per year was visualized and compared with the spatial coverage of mussel farms in Golden Bay, Tasman Bay, and the Marlborough Sounds. Each settlement sampling point was also geographically linked to any operationally active mussel farms within the estimated larval dispersal distance at the time of sampling to test for the specific impact of nearby cultured mussels on settlement rates. The estimated larval dispersal distance, or larval range, was defined as area accessible within 10 km of water travel (i.e. not crossing land) for the narrow confines of the Marlborough Sounds or 25 km within Tasman Bay and Golden Bay (where the maximum distance between a larval monitoring site and mussel farm was 25 km). Different geographic scales were chosen for the locations to reflect the low water exchange in the narrow Marlborough Sounds, where hydrodynamic larval dispersal models have indicated that 90% of mussel larvae settle within 10 km of their source compared to the more open Golden and Tasman Bays, where larvae may travel for much greater distances (N. Broekhuizen pers. comm.). To test whether the presence of nearby cultured mussels may affect settlement, the spatial coverage of mussel farms within the corresponding larval range was compared with the mean settlement of green-lipped mussels at each sampling point using linear regressions for each of the 3 areas. Coefficients of determination (R^2) values are provided for significant linear regressions.

3. RESULTS

3.1. Mussel population abundance and composition

The Marlborough Sounds wild green-lipped mussel population in the early 1960s prior to commercial harvesting was estimated to be between 5 and 6 million mussels, while in 2020 the cultured mussel population in the area was estimated to be over 2 billion (Fig. 2). Commercial harvesting led to a sharp decline in wild mussel populations through the late 1960s and 1970s, after which the advent of the aquaculture industry led to an increase in the standing stock of cultured mussels. Cumulative mussel populations were estimated to be at their minimum in 1974 and 1975, after the bulk of harvesting of wild mussels but prior to the expansion of mussel aquaculture. By the late 1970s, the cultured mussel population surpassed even the size of the wild mussel population prior to harvesting. Estimated cultured mussel populations in 2020 were 16 161 times greater than wild mussel populations in 2020 and 470 times greater than wild mussel populations at their peak in 1960 prior to significant removal by harvesting.

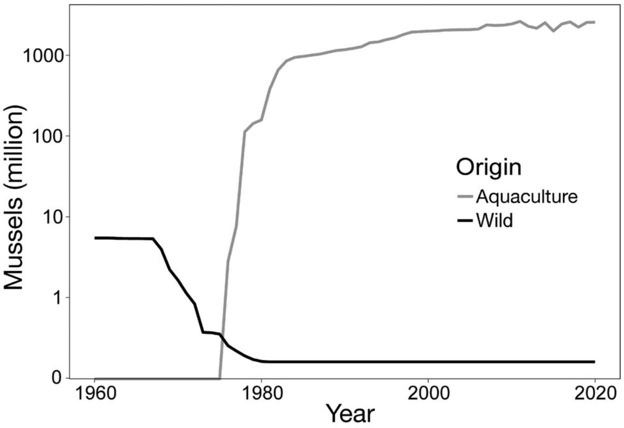

Fig. 2. Estimated mussel populations over time in the Marlborough Sounds, New Zealand. The grey line indicates the estimated total number of mussels at aquaculture sites, and the black line shows estimates of the numbers of wild mussels on the seabed or shoreline (T. A. Toone unpubl. data). Note that the *y*-axis uses a log scale to account for the extreme differences between wild and aquaculture populations

3.2. Mussel settlement

The mean weekly mussel settlement across all sites (Fig. 3A), study areas, and years was 1424 ± 52 (mean ± SE; n = 30 033) mussels per metre of catching rope. Among each of the 3 study areas, weekly mussel settlement was greatest in Golden Bay (3045 ± 143; n = 10 126; Fig. 3B), where it was significantly higher ($p < 0.001$) than in Tasman Bay (1241 ± 144; n = 3299; Fig. 3D) and the Marlborough Sounds (473 ± 12, n = 16 608; Fig. 3F). Annually, the maximum mean weekly mussel settlement per metre of rope was 9868 ± 1353 recorded in Golden Bay in 2013, while the minimum was 30 ± 15 recorded in Tasman Bay in 1999. Overall, variability in mean weekly mussel settlement per year was high throughout the 3 study areas with minimal or no correlation of mussel settlement over the period of the study. Specifically, there were weak negative correlations between settlement and year for the Marlborough Sounds ($\rho = -0.17$, $p < 0.001$) and very weak negative correlations for Golden Bay ($\rho = -0.05$, $p < 0.001$) and Tasman Bay ($\rho = -0.05$, $p = 0.003$).

3.3. Mussel aquaculture expansion

The mussel aquaculture industry began in the Marlborough Sounds in the mid-1970s and expanded steadily for the following 3 decades as the extent of farms continued to increase before plateauing in the 2010s (Fig. 3G). Commercial mussel farming in Golden Bay began later with small-scale farms in the 1990s and larger farms only after 2008 (Fig. 3C), while mussel aquaculture in Tasman Bay did not begin until 2006 and expanded when permits were granted to large farms in 2008 (Fig. 3E).

Collectively for all 3 areas, there were 622 mussel farms in 2020, covering a total of 6275 ha (Fig. 1). Over 92 % of mussel farms were located in the Marlborough Sounds (n = 575) compared to 6 % in Golden Bay (n = 37) and 2 % in Tasman Bay (n = 10). However, the average farm size was much smaller in the Marlborough Sounds (5.1 ha compared to 65.4 ha in Golden Bay and 89.6 ha in Tasman Bay); therefore, only 47 % of the total mussel aquaculture area in

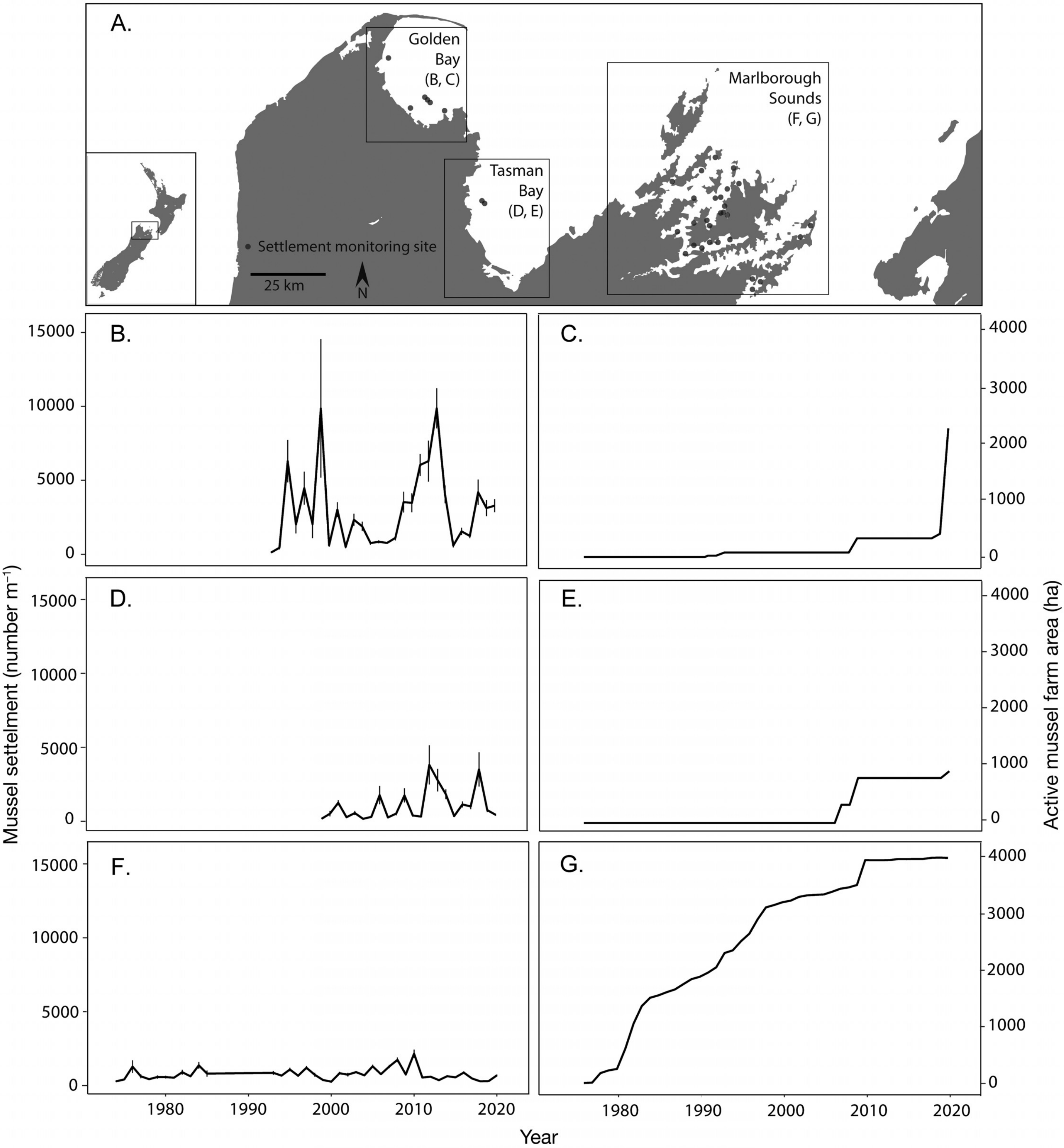

Fig. 3. Mean mussel settlement and total area of active mussel aquaculture in the study region. (A) Settlement monitoring sites (grey circles) in the major areas in the study region. (B,D,F) Mean weekly green-lipped mussel settlement per metre of sampling rope in each area per year. Error bars show SE. (C,E,G) Total area of mussel aquaculture under active permit in each study area per year

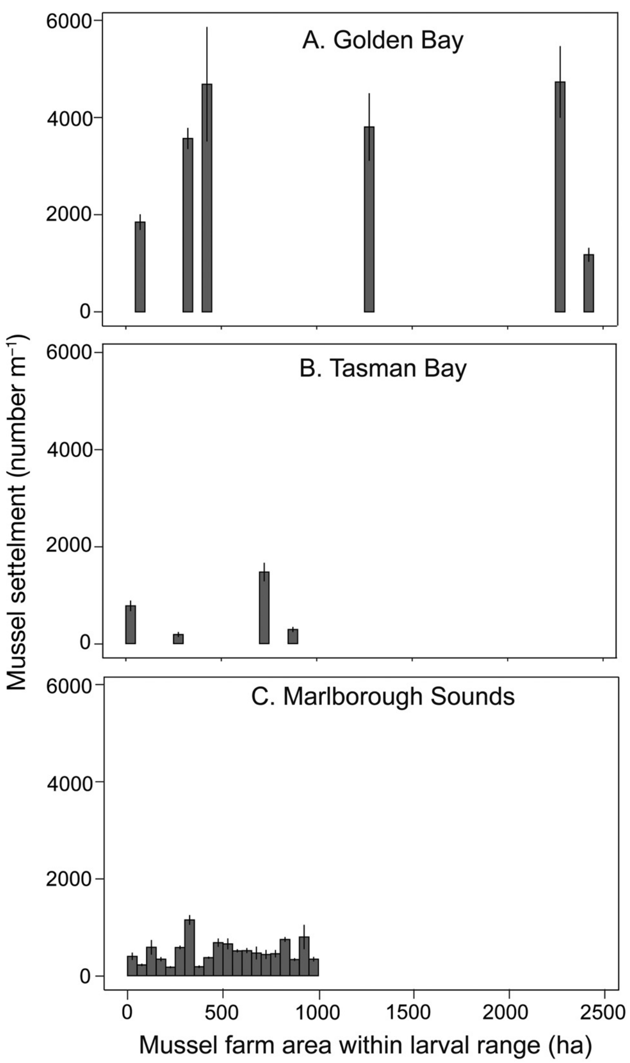

Fig. 4. Mean mussel settlement and corresponding total extent of nearby mussel aquaculture. Mean green-lipped mussel settlement per metre of sampling rope (n = 16 563) from 1974 to 2020 in (A) Golden Bay, (B) Tasman Bay, and (C) the Marlborough Sounds compared with total area of mussel aquaculture within the estimated larval dispersal distance for each study area (25 km of the sampling location for Golden Bay and Tasman Bay or 10 km for the Marlborough Sounds). Error bars show SE

2020 was in the Marlborough Sounds (2958 ha) while 39% was in Golden Bay (2421 ha) and 14% in Tasman Bay (896 ha).

3.4. Mussel settlement and aquaculture comparisons

The Marlborough Sounds contained the greatest area of mussel farms in any given year, but recorded low settlement, statistically similar to the settlement recorded in Tasman Bay ($p < 0.001$) despite far lower coverage by mussel farms in Tasman Bay. Conversely, Golden Bay recorded significantly greater mussel settlement than either of the other 2 regions ($p < 0.001$) despite only a very recent increase in the extent of mussel aquaculture. On a more granular scale, the highest average settlement rate across all study areas was recorded when there were 2250–2300 ha of active mussel farms within larval range, resulting in an average catch of 4730 ± 737 mussels per metre of rope, and the lowest settlement was recorded when there were 200–250 ha of mussel farms within larval range resulting in 176 ± 21 mussels per metre of rope (Fig. 4). Overall, there was no significant effect of aquaculture area within larval range on mussel settlement for Golden Bay ($p > 0.05$) or Tasman Bay ($p > 0.05$) and a significant ($p = 0.03$, $F = 4.55$), but ecologically non-existent (adjusted $R^2 = 0.0002$), positive effect for the Marlborough Sounds.

4. DISCUSSION

Comparing *in situ* mussel settlement with changes in the extent of mussel aquaculture revealed that the influence of shellfish aquaculture on local settlement was non-existent. Mussel settlement data covering a 47 yr timespan showed, at most, only trivial correlations between settlement and aquaculture expansion in the study region, and no increases commensurate with the estimated 16 000-fold increase in mussel abundance following the dramatic expansion of mussel aquaculture in the 1980s and 1990s. Additionally, there is no clear indication that the cultured mussel population is acting as a significant net consumer of settling larvae because settlement prior to the expansion of mussel aquaculture is generally comparable to post-farming settlement. Furthermore, settlement recorded at sites adjacent to extensive mussel aquaculture was statistically similar to settlement at sites with no adjacent mussel aquaculture.

Previous biophysical modelling and trace elemental fingerprinting indicated that mussel aquaculture in northern New Zealand could provide a source of larvae capable of settling throughout the surrounding environment (Norrie et al. 2020). However, it was not possible in this previous study to distinguish whether the captured settled mussels were sourced from broodstock in aquaculture or wild populations. If production from cultured mussels is contributing to larval supply, as suggested by Norrie et al. (2020), then it would be expected that larval settlement would have increased markedly with the expansion of mussel aquaculture observed in the 3 distinct areas analysed in this study. This was not the case, as mussel settlement showed no substantive long-term trends for any of the 3 areas examined. This discrepancy confirms the importance of supplementing modelling-based techniques with *in situ* data like the kind used in this study and reflects the inherent difficulties in accurately modelling mussel settlement in complex real-world ecosystems (Gawarkiewicz et al. 2007, Nolasco et al. 2018) as well as the potential disconnects between larval supply and mussel settlement reported elsewhere (Porri et al. 2006, Pineda et al. 2010).

The lack of long-term trend in mussel settlement, despite an overall increase in the total population of mussels by 4 orders of magnitude as a result of aquaculture expansion, could have several possible explanations. For example, green-lipped mussels are known to cannibalize larvae and juveniles, which compose up to 70% of the food particles in wild mussels in northern New Zealand (Alfaro 2006). This cannibalistic diet has not been studied in farmed mussels, but it is possible that the 3-dimensional nature of mussel aquaculture, suspended in the water column, may result in larvae more quickly being consumed by the surrounding filter-feeding adult mussels to reduce the abundance of settling larvae. Therefore, mussel aquaculture could serve both as a producer and consumer of larvae rather than only one or the other, counterbalancing to produce the minimal net effect in mussel settlement observed in this study. However, there is little evidence of this counterbalancing occurring given the lack of relationship between the scale of mussel settlement in relation to the extent of adjacent mussel aquaculture, as it would be expected that larvae approaching settlement size would be more likely to be consumed in waters adjacent to areas with extensive mussel aquaculture and yet there was no clear decrease in settlement in the vicinity of mussel farms.

Alternatively, aquaculture mussels may contribute substantially to the larval population, but also reduce food availability (Duarte et al. 2008) or otherwise impact the carrying capacity of the environment (Wijsman et al. 2018), resulting in a net-neutral impact on larval survival and settlement over time. Again, this scenario seems unlikely given the lack of relationship between the scale of settlement in relation to the extent of adjacent mussel aquaculture. Previous studies have demonstrated that reductions in phytoplankton abundance associated with mussel aquaculture are localised in extent (Gall et al. 2003, Pinkerton et al. 2018), suggesting that any effect on larval performance would be in the immediate vicinity of aquaculture. For example, concentrations of plankton were estimated to be reduced by around 8–10% within a few kilometres of a large and concentrated area of mussel aquaculture in northern New Zealand (Broekhuizen et al. 2004, 2005, Stenton-Dozey et al. 2005), which may impact larval success in that same area. However, in the areas analysed for this study, mussel settlement was not found to be reduced within the vicinity of mussel aquaculture, suggesting the impacts of this plankton reduction are not driving settlement rates.

More plausibly, environmental or biological factors may either prevent aquaculture mussels from producing larvae or make them inviable in local conditions. Throughout the 3 study areas, mussel settlement was relatively high even before the arrival of any prominent mussel aquaculture activity, suggesting that the remnant wild mussel populations following overharvesting are capable of sustaining substantial mussel settlement rates. This is further supported by the large reproductive capacity of green-lipped mussels, as a single female can produce up to 100 million eggs in a season (Jenkins 1985). The settlement observed over the past 4 decades, then, may be a result of only small, remnant, wild populations. There are marked differences between wild and cultured mussels that may account for a discrepancy in larval production or survival between the 2 groups. Cultured mussels are typically harvested at around 2 yr of age (Dawber 2004), when they are typically between 90 and 110 mm (Jeffs et al. 1999), have a high meat-to-shell ratio (Hickman & Illingworth 1980), and have not yet spawned for the current season (Dawber 2004). In contrast, wild green-lipped mussels can live for decades, grow to over 200 mm (Jenkins 1985), and have a lower meat-to-shell ratio (Hickman & Illingworth 1980).

Since the 1980s, mussel aquaculture in the study region has used large quantities of wild seed mussels transported from northern New Zealand to facilitate aquaculture expansion that was not possible from seeding with the insufficient locally caught wild seed supply (Dawber 2004). Northern mussels come from a different environment (Ren et al. 2019), are genetically distinct from wild mussel populations in the study areas (Gardner et al. 1996, Apte et al. 2003), and have a different breeding periodicity (Alfaro et al. 2001, 2003). One or more of these differences may result in an inability of the cultured mussels derived from imported northern seedstock to effectively contribute to larval supply in this non-natal region. For example, differences in breeding periodicity, such as the extended spawning season for northern mussels compared to southern mussels (Alfaro et al. 2001), may lead to a disconnect with other important environmental parameters like seasonal macroalgae required for settlement. Ultimately, identifying the cause of the disconnect between the scale of mussel aquaculture and settlement in this region will rely on fine-scale determination of larval viability and source, which is increasingly possible through high-resolution molecular methods (Kim & Roe 2021).

5. CONCLUSIONS

Both cultured and wild shellfish populations rely on abundant mussel settlement; however, a 16 000-fold increase to local mussel populations as a result of enormous aquaculture growth appears to have had, at most, a trivial impact on mussel settlement at the northern end of New Zealand's South Island. If mussel aquaculture is not contributing significantly to the local mussel settlement as suggested by these data, then it is vital for further research to confirm and recognize the role of existing wild shellfish populations as dominant sources of shellfish settlers even in systems where they are vastly outnumbered. Maintaining and restoring these wild populations not only provides the ecosystem services traditionally associated with shellfish reefs, but may also enhance larval settlement to the benefit of local aquaculture interests. If remnant reefs are still producing a substantial supply of settling larvae, then restoring even relatively small populations has the potential to dramatically increase this same supply. For example, in this study region, mussels are at less than 3 % of historical levels in some areas, so restoring just an additional few percentage points of mussels may have outsize impacts on the source population for existing mussel settlers. In turn, enhanced larval settlement may initiate the natural recovery of other extirpated local reefs and support the aquaculture industry that currently relies on seed stock transported from across the country. In light of these findings, both conservation and aquaculture interests would benefit from supporting efforts to restore wild shellfish reefs, and in turn, improve local settlement and the corresponding economic, ecological and environmental benefits.

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