Understanding and mitigating seaweed forest change in Aotearoa New Zealand

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Understanding and mitigating seaweed forest change in Aotearoa New Zealand

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Prepared for Envirolink with Hawke's Bay Regional Council and Environment Southland

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Executive summary

This project examined if seaweed forest community distribution and abundance have changed in Aotearoa New Zealand, and if so, how changes have impacted people who are associated with seaweed habitat. To achieve this, a collaboration was formed between Cawthron Institute in Aotearoa New Zealand and University of California Santa Barbara Bren School of Environmental Science & Management in the United States. The project was supported by Hawke's Bay Regional Council and Environment Southland through a medium Envirolink grant and was structured around two pillars. The first pillar was to identify any trends or changes in the distribution and abundance of seaweed forest communities in Aotearoa New Zealand. This work was based on robust biological surveys conducted across three regions – Pānia Reef (Hawke Bay), Lyttelton Harbour / Whakaraupō (Canterbury) and Fiordland (Southland) – and aimed to understand how sea temperature and geographic factors influence seaweed forest habitat. For the second pillar, we assessed the social and cultural dynamics surrounding how tangata whenua in Te Tauihu Te-Waka-a-Māui (top of the South Island, hereafter Te Tauihu) value coastal resources and whether they have observed changes in local rimurimu (seaweed) forests in the region.

We found that changes in seaweed community composition were specific to each region and to the depth gradient of the reef. For example, in Lyttelton Harbour, there was an increase (about 20% cover) in canopy-forming seaweed abundance for multiple species at shallow (3–5 m) sites. However, at the deeper sites (6–8 m), there was approximately 15% loss of canopy-forming seaweed cover between 2016 and 2024. Over the same period at Pānia Reef, there was a slight increase in abundance of subcanopy brown (average cover rank increased from 0.4 to 1.0), red (average cover rank increased from 2.4 to 3.2) and green (average cover rank increased from 0.0 to 0.6) seaweeds but a decline in the abundance of canopy-forming seaweed (average cover rank decrease from 2.11 to 1.21). In Fiordland, seaweed community composition and changes of abundance over time were most dependent on the depth of the rocky reef. For example, there was a greater abundance of subcanopy red, green and brown seaweeds in the intertidal and shallow subtidal (2–4 m) habitat (12.4% average red subcanopy cover; 8.7% average green subcanopy cover; and 3.5% average brown subcanopy cover) compared to the deeper (> 7 m) rocky reef habitats (2.4% average red subcanopy cover; 5.2% green subcanopy cover; and 0.5% average brown subcanopy cover). There were also fiord-specific effects between both fiords (Milford Sound and Doubtful Sound); for example, there was more subcanopy red seaweed in Doubtful Sound (23.7% average red subcanopy cover compared to 12.4% in Milford Sound) and more subcanopy brown seaweed in Milford Sound (4.6% average brown subcanopy cover compared to 2.4% in Doubtful Sound). Yet, over the two decades of study (2006–24) and across both fiords, there was a general decline of subcanopy red seaweed, particularly in the intertidal and shallow subtidal habitat (a decrease from 18.4% to 12.4% average cover from intertidal to 4 m depth). Canopy-forming seaweeds were found in low abundance in Fiordland and generally at depths greater than 7 m.

We observed a rising trend in seawater temperatures over the past two decades, along with increasing sea surface temperature (SST) anomalies across all three regions over the same period. The literature provides evidence that rising seawater temperature, and extreme SST

anomalies, such as marine heatwaves, negatively affect seaweed community composition and abundance. We suspect that similar negative trends between SST anomalies and seaweed community composition and abundance also occur within the three studied regions, potentially mediated by depth. We found a decline in subcanopy red and brown seaweeds at the shallow sites in Lyttelton Harbour during periods when seawater temperature was higher than average, whereas deeper sites at both Lyttelton Harbour and Pānia Reef did not exhibit similar trends. We also found a decline in subcanopy red seaweed on intertidal and shallow subtidal reefs in Milford and Doubtful Sounds from 2019 to 2025. This may correlate with rising seawater temperatures, with average SST anomalies of 3 °C higher in 2022 and 2023 than previously recorded. However, we did not statistically test the frequency or intensity of SST anomalies against changes in seaweed community composition. We suggest these exploratory trends warrant further investigation. Additionally, we found evidence of negative effects from a cyclone on seaweed composition and abundance at Pānia Reef. Following Cyclone Gabrielle in 2023, declines were observed in canopy-forming, subcanopy brown and subcanopy red seaweeds. Extreme weather events will likely confound relationships between changes in seaweed abundance and composition, and SST anomalies. Nevertheless, these compounding pressures – warming seawater temperatures and increasing extreme storm events – are expected to impact seaweed communities and associated habitats. We recommend that future analyses of these seaweed community data also examine changes in seaweed communities and abundances in relation to varying levels of coastal sedimentation, given the overwhelming evidence for its negative effects on coastal communities.

Following an informative and engaging hui with tangata whenua in Te Tauihu, hosted by Te Ātiawa O Te Waka-A-Māui Trust, we released an online survey to assess the social and cultural dynamics surrounding seaweed forests. Due to the relatively low response rate (19 respondents) for the survey, a statistical analysis was not conducted. However, among those who responded, the majority demonstrated a strong engagement with Māori culture. Most participants indicated that they value the environment and taonga (treasured or culturally revered) species and were concerned about climate change. Many also considered commercial fishing to have a negative impact on their family’s ability to fish. However, most respondents believed that commercial seaweed aquaculture would at least have a moderate positive impact on their livelihood. Lastly, the majority felt that land-use practices have had a negative impact on seaweed forests.

Results from this collaborative project provide insights into changes in seaweed forests in Aotearoa New Zealand. Notably, we highlight habitat and seaweed functional groups that may be more vulnerable to a changing climate, specifically increasing seawater temperatures. These findings aim to help coastal managers protect important foundational seaweed species and identify resilience among seaweed communities. This project also highlights the importance of linking people and environment within coastal communities to share knowledge and help manage these dynamic, highly prized ecosystems.

1. Introduction

Seaweed forests are 'extensive underwater habitats' defined by large seaweeds that form canopies over the seafloor (Schiel and Foster 2006; Wernberg et al. 2019). Like trees in a forest, seaweed provides food, shelter, nursery ground and habitat for many organisms, including commercially important species such as rock lobster and abalone (Wernberg et al. 2019; Cornwall et al. 2023). Seaweed forests form crucial and biodiverse ecosystems, potentially mitigate ocean acidification effects at local scales, reduce marine pollution via nitrogen and carbon sequestration, and boost local economies through ecotourism (Eger et al. 2022; Cornwall et al. 2023).

Seaweed forests are globally declining from the direct and indirect effects of anthropogenic activities (Wernberg et al. 2019), which include poor land-use practices that result in high coastal sedimentation and smothering of seaweeds (Airoldi 2003; Tait et al. 2021), as well as disruption of trophic cascades, causing over-grazing by herbivores (Ling et al. 2015). However, in this study, we focus on the effects of ocean warming and sea surface temperature (SST) anomalies, such as marine heatwaves (MHW), which have been correlated with reduced nutrient availability (Zimmerman and Kremer 1984; Edwards and Estes 2006; Cavanaugh et al. 2021).

Ocean warming is caused by the oceanic absorption of vast quantities of heat from increased concentrations of greenhouse gases into the atmosphere, mainly from fossil fuel consumption (Laffoley and Grimsditch 2009; Lindsey and Dahlman 2025). MHW are discrete anomalous warm seawater events that can 'substantially affect marine ecosystems' and can result from a combination of local oceanic and atmospheric processes such as 'air-sea heat flux' and 'horizontal temperature advection' (Oliver et al. 2021). The global count of MHW days per year has risen between 1925 and 2016 due to increases in MHW duration and frequency (Oliver et al. 2018). For example, over this period, there was an increase of 34% and 17% in the global average MHW frequency and duration, respectively, and overall, this has resulted in a 54% increase in annual MHW days around the world (Oliver et al. 2021). This trend is projected to increase further under climate change as a 'consequence of long-term ocean warming' (Oliver et al. 2021; IPCC 2022).

Marine heat waves can cause mass mortality of marine species and economic damages totalling billions of dollars (Smith et al. 2023). In Aotearoa New Zealand, elevated temperatures have exhibited negative impacts on seaweed forests (Thomsen et al. 2019; Tait et al. 2021; Cornwall et al. 2023). Similarly, in southern California, studies demonstrated that increasing seawater temperatures can impact fundamental mechanisms in seaweeds, driving forest losses through limited nutrient availability associated with warmer waters (Zimmerman and Kremer 1984; Edwards and Estes 2006; Cavanaugh et al. 2021). Seaweed species, such as *Macrocystis pyrifera* (giant bladder kelp), depend on reliable nitrogen input to survive (Gerard 1982; Edwards and Estes 2006). MHW events lead to deeper thermoclines, which can affect the survival of seaweed forests by interfering with the upwelling of cold, nutrient-rich waters (Edwards and Estes 2006).

The loss of seaweed forests around the world (Krumhansl et al. 2016) is of particular concern because of the historical use of seaweed-related resources dating back thousands of years (Erlandson et al. 2007). For example, tangata whenua of Aotearoa New Zealand have consumed highly nutritious red and green seaweeds and used the blades of bull kelp (*Durvillaea* spp. or rimurapa) to create food storage bags (Wassilieff 2009). Before European arrival, a primary food source came from 'gathering seafood during low tide in the sand or on rocky shores'. These food types are still an important dietary component for many people in Aotearoa New Zealand and can be specific to location, iwi and hapū (Fox 2010). Harvesting seafood (or kaimoana) is an integral part of Māori culture, where various techniques and locations (mahinga kai) for acquiring seafood are passed down through generations (Fox 2010).

Research in Aotearoa New Zealand has shown marked declines in the distribution of seaweeds, particularly on the east coast of the South Island (Thomsen et al. 2019; Tait et al. 2021). In response to degrading seaweed habitats, researchers in Aotearoa New Zealand are studying seaweed restoration and propagation methods, including aquaria experiments on the effects of increased seawater temperatures on seaweed life cycles (Nelson 2005; Le et al. 2022; Crossett et al. 2023). Understanding how rising seawater temperatures affect the early life stages of important canopy-forming seaweeds will be informative for seaweed community resilience and active restoration of degraded seaweed ecosystems (Eger et al. 2022).

1.1 Project objectives

This project examined whether seaweed forest composition and abundance have changed in Aotearoa New Zealand, and if so, how these changes have impacted people and the environment. To achieve this, we structured the project around two pillars. First, we sought to identify trends in seaweed forest changes based on robust biological surveys conducted by Cawthron scientists across three regions of Aotearoa New Zealand. These surveys aimed to understand the environmental and geographic factors influencing seaweed forests. Second, we aimed to recognise the rights and interests of Māori and their deep connection to coastal resources. To investigate this, Cawthron organised an in-person hui, and Te Ātiawa O Te Waka-A-Māui Trust hosted this hui in Waitohi (Picton) to engage with tangata whenua about rimurimu (seaweed) change in Te Tauihu Te-Waka-a-Māui (the top of the South Island, hereafter Te Tauihu). Following the hui, an online survey was conducted to assess the social and cultural dynamics influencing how tangata whenua in Te Tauihu value coastal resources and perceive the impact of current marine resource management.

2. Seaweed forest distribution over time and the effect of sea temperature on communities

Seaweed forests are declining globally at an annual rate of approximately 2% cover (Wernberg et al. 2019), in part due to increased SST (Hollarsmith et al. 2020). The significant threat of heat-related disturbance events to seaweed forest ecosystems located on temperate rocky reefs has been documented across various countries, including Australia (Bulter et al. 2020), Aotearoa New Zealand (Thomsen et al. 2019; Tait et al. 2021; Cornwall et al. 2023) and the United States (Rogers-Bennett and Catton 2019). MHW, often driven by climate change, are associated with extensive losses of seaweed forest ecosystems, as observed in California, Unites States, from 2014 to 2017 and Aotearoa New Zealand from 2017 to 2018 (Rogers-Bennett and Catton 2019; Thomsen et al. 2019; Tait et al. 2021). The destructive impacts observed from MHW in Aotearoa New Zealand mirrored those in California, where SST increased by over 2.5 °C above the average for an unprecedented 226 days. The parallels between the studied impacts of MHW underscore the need for further interpretation and analysis of monitoring data to understand how these critical ecosystems respond to climatic and ocean dynamic changes.

To investigate the effect of SST change on seaweed forests, long-term seaweed forest community data are necessary. For this project, the community composition data were provided by the Cawthron Institute and sourced from areas that extend beyond those studied in the existing literature. It encompasses a range of locations representative of Aotearoa New Zealand's coastline, providing broad spatial coverage for ecological assessment. Analysis of these data, combined with SST and SST anomaly[1] data provided by National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch,[2] will help understand the impacts of changing SST, particularly changes that are anomalies, on seaweed forest communities across a wider geographic range. Furthermore, this approach will allow for comparisons between different regions of Aotearoa New Zealand. The project aims to provide critical evidence of the extent of impacts associated with warming events (specifically SST anomalies) on seaweed abundance and community structure, addressing gaps in the literature on the regional variability of climate change effects on coastal ecosystems in Aotearoa New Zealand.

2.1 Research questions

The two research questions that guided the project's investigations were:

1. How does the community composition of seaweed forests vary across different coastal locations in Aotearoa New Zealand?
2. Has there been an average change in seawater temperature or number of SST anomalies over the period the biological community data were collected to inform on seaweed community compositions for this study?

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[1] The difference between present-day SST and the historical average, ranging from −5 °C to +5 °C

[2] NOAA Coral Reef Watch Homepage and Near Real-Time Products Portal

2.2 Methods

Survey sites and data collection

Dive surveys were performed by scientific divers from the Cawthron Institute (Cawthron) as part of various compliance monitoring across three locations in coastal Aotearoa New Zealand: Port of Napier (Pānia Reef) from 2016 to 2024, Lyttelton Harbour / Whakaraupō (hereafter Lyttelton Harbour) from 2016 to 2024, and Fiordland from 2006 to 2024 (Figure 1). Pānia Reef, located off the Port of Napier, is on the east coast of the North Island in the Hawke's Bay Region; Lyttelton Harbour is on the east coast of the South Island in the Canterbury Region; Fiordland is on the southwestern coast of the South Island in the Southland Region. The Fiordland location includes two fiords (Milford Sound / Piopiotahi [hereafter Milford Sound] and Doubtful Sounds / Pātea [hereafter Doubtful Sound]), both receiving high freshwater input. This selection of sites allows for a comprehensive evaluation of temperate rocky reef ecosystems across diverse environmental conditions, which contributes to the understanding of nationwide habitat trends.

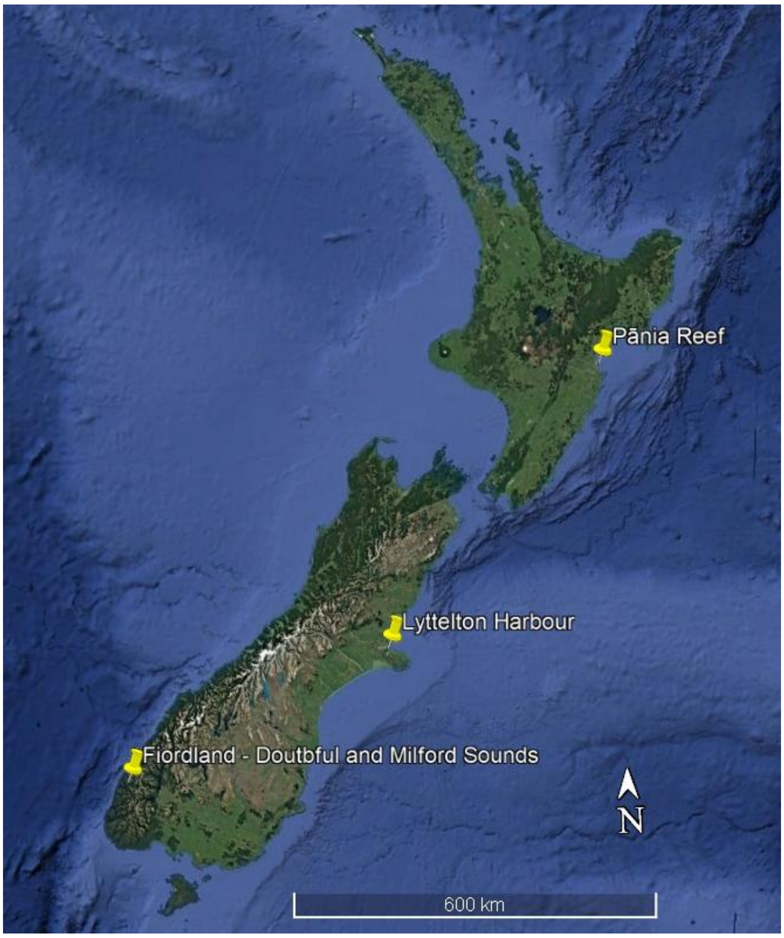

Figure 1. Dive survey sites in the North and South Islands of Aotearoa New Zealand. The yellow points indicate the three locations: Pānia Reef (Hawke Bay), Lyttelton Harbour / Whakaraupō (Canterbury), Fiordland (Southland). Source: Google Earth Pro software.[3]

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[3] Imagery data: 14 December 2015.

Pānia Reef (Port of Napier)

Pānia Reef is a prominent seabed feature in southern Hawke Bay (Duffy 1992). The reef extends to the northeast, beginning approximately 800 m from the Port of Napier (Figure 2). It is widest at the southwestern end (about 400 m), approximately 1 km northeast of the leading port breakwater, where the boulder and rock substrate emerges gradually from a 15 m deep sand bottom. Towards the seaward end, the topography becomes progressively steeper, with large rocks that are fissured with crevices protruding from a sandy seabed at 18 m water depth. Eight dive surveys were conducted at Pānia Reef between April 2016 and October 2023 to monitor marine ecosystems, establish baseline conditions, and document if there were any ecosystem changes resulting from this dredging project.

For each survey, eight 100 m transects were run along Pānia Reef and tagged at 10 m intervals. Biological community data were collected for each 10 m interval and 1 m either side of the transect line (Figures 2 and 3). Each survey recorded water depth in metres, habitat / substrate type (bedrock, boulders, cobble, shell hash, silt, sand / gravel or bare), and relative abundance of algal and faunal species, including fish and invertebrates, using the ordinal scale described in Table 1. Video footage was taken with a GoPro between each of the 10 m distance tags. In addition to video footage, both divers had hand-held compact cameras to photograph species. Video and photo media were used to complement the data compiled in the field.

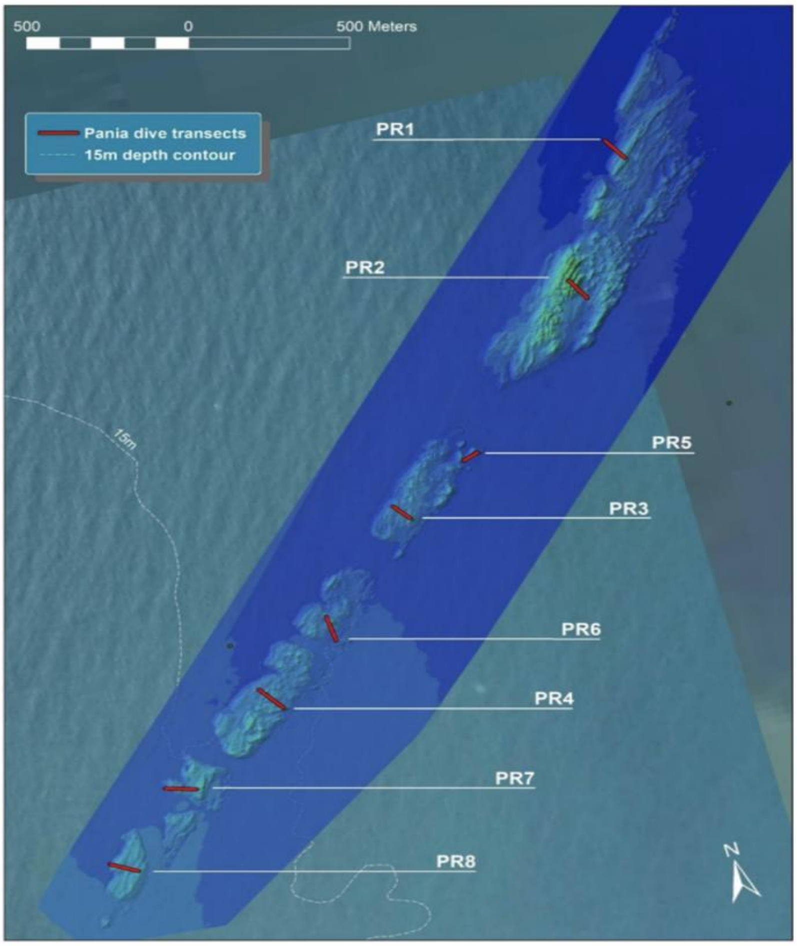

Figure 2. Location of eight sites (PR1–PR8) across Pānia Reef. Source: Sneddon and Crossett (2024).

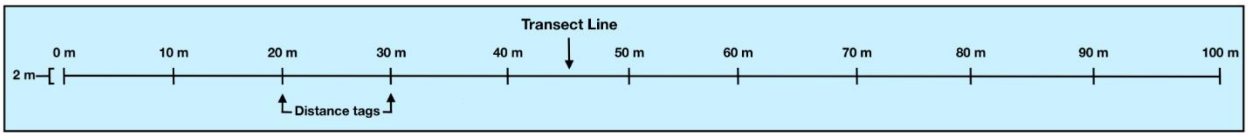

Figure 3. Pānia Reef transect intervals. Each transect laid along Pānia Reef was 100 m long and divided into ten 10 m intervals identified by distance tags. Data were recorded at each interval of each transect. Source: Sneddon and Crossett (2024).

Table 1. Description of ordinal seaweed forest abundance scale (Source: Sneddon and Crossett 2024).

Category	Rank value	Description
Absent	0	Not observed
Rare	1	1–2 individuals, or a single cluster or patch of individuals in one small area (e.g. small patch of sponge or algae)
Occasional	2	3–10 individuals throughout the (2 m × 10 m) area of assessment
Common	3	> 10 individuals throughout the (2 m × 10 m) area of assessment
Abundant	4	Individuals abundant enough to form a distinct zone or habitat (e.g. mussels, barnacles and some algae), or hundreds to thousands of individuals per m^2

Lyttelton Harbour and Banks Peninsula (Port Lyttelton)

Lyttelton Harbour is a natural harbour on the Banks Peninsula in the Canterbury Region of Aotearoa New Zealand's South Island. It is Christchurch's main port and is vital for maritime trade, hosting cargo shipping, fishing and recreational boating activities. The harbour supports diverse marine habitats, including rocky reefs and soft sediment environments. The area is also a focal point for conservation and ecological restoration efforts, as it holds ecological significance and is of cultural importance to Ngāi Tahu iwi.

Thirteen dive surveys were conducted in Lyttelton Harbour and Banks Peninsula between February 2016 and September 2024 to establish baseline conditions of benthic habitats and monitor if the dredging project, implemented by the Lyttelton Port Company Ltd, had an effect on the associated habitat. For each survey conducted, 30 m subtidal transects were laid at six locations (Figure 4). At each location, a 100 m offshore transect was positioned, and two 30 m transects – one deep (6–8 m) and one shallow (3–5 m) – were laid perpendicular to the 100 m transect line, roughly parallel to the shore (Figure 4A). Two locations, LH07 and BP13, were unsuitable for a deep (6–8 m) transect line, so only shallow transect lines were surveyed at these locations. Along each of the 30 m transects, eight 1 m^2 quadrats were haphazardly placed (Figure 4A). Water depth (metres) was measured from wrist-mounted dive computers at each quadrat. Additionally, the estimate of percentage cover of substrate type (bedrock, boulders, cobble, shell hash, silt, sand / gravel or bare), canopy-forming and understory algae, and encrusting invertebrates were assessed along with counts of solitary epifauna (Sneddon and Dunmore 2021).

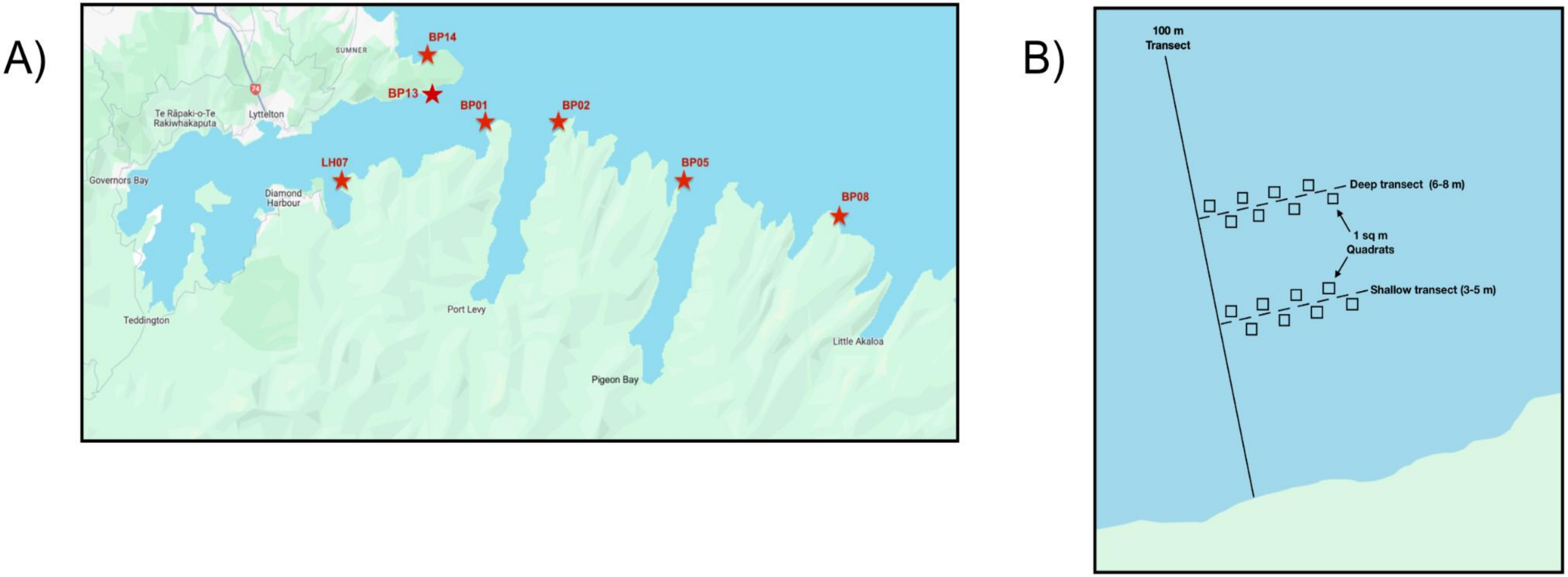

Figure 4. Dive survey transects locations and layout in Lyttelton Harbour / Whakaraupō. (A) Locations of each dive survey are marked by a red star. All locations contained a deep and shallow transect, except sites LH07 and BP13, which only had shallow transects. (B) Design of layout for deep (6–8 m) and shallow (3–5 m) transects established at each dive survey location. Source: Sneddon and Dunmore (2021).

Fiordland (Meridian)

Eight intertidal and subtidal sites have been surveyed in Doubtful Sound since 2006, and three in Milford Sound since 2007 (Figure 5). Both fiords are part of Fiordland National Park and Te Wahipounamu, a UNESCO World Heritage site.[4] Milford Sound serves as a reference point for comparison with Doubtful Sound. Manapōuri Power Station, operated by Meridian Energy, releases water diverted from Lake Manapōuri and discharges it into the head of Doubtful Sound (Crossett et al. 2024). Cawthron was contracted by Meridian Energy to survey the Fiordland sites (Crossett et al. 2024). These two fiords are collectively referred to as Fiordland in this section.

Fiordland includes focus sites, which are continuously surveyed, and non-focus sites, which were surveyed at the pilot stages (Figure 5). For this study, only focus sites are evaluated because of their greater temporal consistency. Each focus site included three different data types: intertidal, transitional and subtidal. Intertidal data were collected between low and high tide zones at each site and are indicated by numbered sites (Figures 5A and 5B). Transitional data included surveying intertidal areas from inner to outer fiords, representing different zones where intertidal communities transition from one group to another (e.g. barnacles to mussels) (Figures 5C and 5D). Lastly, subtidal data were collected at depths of 2, 4, 7, 10 and 16 metres at various points across the fiords, covering the same numbered locations as the intertidal data. All data were collected with a GoPro camera and associated standardised photo-quadrats of 0.25 m^2. Images were analysed by Cawthron scientists to assess percentage cover of sessile species, such as seaweed, and counts of mobile species, such as gastropods and urchins.

Water temperature was monitored from two mooring buoys, M1 and M4, within each fiord, as illustrated by the yellow triangles (Figures 5A and 5B). These temperature mooring buoys have been operational since 2005, collecting data every 30 minutes across a 25 m depth profile (0.5, 1, 1.5, 2, 3, 5, 7, 9. 11, 14, 19 and 25 m). There were small gaps in the mooring temperature due to technical errors, maintenance or extreme weather conditions.

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[4] https://whc.unesco.org/en/list/551

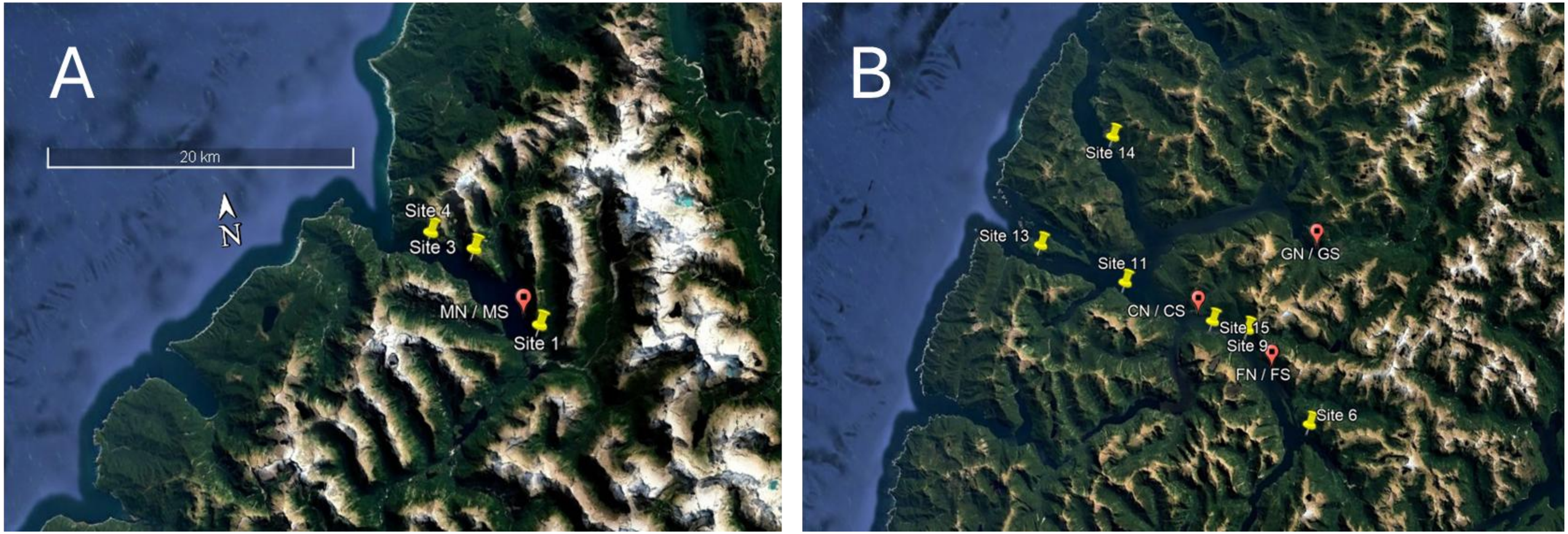

Figure 5. Focus sites (yellow pins) and transitional sites (red pins) of (A) Milford Sound / Piopiotahi and (B) Doubtful Sound / Pātea. (A) Approximate locations of focus and transitional sites of Milford Sound. (B) Approximate locations of all focus and transitional sites in Doubtful Sound. Source: Google Earth Pro software.[5]

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[5] Imagery data: 14 December 2015.

Seaweed functional group categorisation and data organisation

Species were categorised based on taxonomic group definitions provided by Cawthron scientists along with combined phyla and class-level classifications. Seaweed species were further classified into functional groups – canopy, subcanopy (red, green, brown), floor species and epiphytes – using both ‘New Zealand seaweeds: an illustrated guide’ (Nelson 2020) and expert insights from Cawthron scientists (Table 2). Functional groups were defined by their structural and ecological roles in a seaweed forest ecosystem. The canopy group consisted of large, surface-reaching seaweed, such as *Macrocystis pyrifera* and *Ecklonia radiata*, which provide habitat complexity and primary productivity. The subcanopy included smaller understory seaweeds, such as *Rhodymenia* spp., *Zonaria* spp. and *Ulva* spp., which grow beneath the canopy, contributing to vertical structure and shade. Floor species were composed of turfing algae, which form dense, low-growing mats, and encrusting algae species, which grow as thin layers over hard substrates. Lastly, small algae and invertebrates that grew on the surfaces of larger seaweeds or other substrates were categorised as epiphytic organisms.

Table 2. Seaweed functional group and subgroup classifications. Seaweed taxa from all surveyed sites were categorised into functional groups and subgroups. Note that not all species listed in this table were present in all three sites.

Functional group	Subgroup	Species
Canopy	**Phaeophyta**	*Ecklonia radiata*, *Macrocystis pyrifera*, *Carpophyllum maschalocarpum*, *Carpophyllum flexuosum*, *Landsburgia quercifolia*, *Undaria pinnatifida*, brown blade recruits
Subcanopy	**Rhodophyta**	Red branching *Rhodophyllis*, red filamentous algae, feather red *Plocamium*, red feathery *Ballia*, red feathery *Euptiloda*, foliose red algae, Rhodophyta sp., red fine algae, *Ceramium*, *Rhodymenia* spp., *Plocamium* spp., *Pterocladia* sp.
	Chlorophyta	*Codium*, fine green filamentous, *Ulva lactuca*, Chlorophyta
	Phaeophyta	*Halopteris*, brown alga filamentous, *Dictyota* spp., *Desmarestia*, *Zonaria*, *Carpomitra costata*
Floor species	**Turfing**	Fine green moss-like alga, coralline turf, fine turfing red algae, brown turfing algae
	Encrusting	*Microzonia*, brown encrusting algae, coralline paint, *Rhizopogonia* red prostrate blades, *Microzonia velutina*, corallinales, red encrusting algae

Seaweed abundance was measured using different methodologies at each of the study locations. Surveys in Lyttelton Harbour and Fiordland used percentage cover, while an ordinal scale was used in surveys at Pānia Reef (Table 1). To enable cross-site comparisons between the surveys conducted in

Lyttelton Harbour and Pānia Reef, percentage cover data were converted to the ordinal scale using definitions provided by collaborators at Cawthron (Table 3). Fiordland sites had six different depths of data collection across multiple survey types. Converting these surveys to ordinal data would greatly dilute the specificity that could be achieved with percentage occurrence data from both fiords of Fiordland; therefore, the ordinal scale conversion was not applied to data from these sites.

Zero-inflated observations are common in ecological survey data, i.e. many taxa are often not observed at a site. To address the zero-inflated nature of our data, we created two versions for each dataset. The first, termed 'presence-only', excluded all zero values, retaining only instances where observations were recorded. The second, termed 'presence–absence', converted abundance data into a binary format. With this binary method, values greater than zero were recorded as present (1), and zero values were recorded as absent (0).

Table 3. Guide for converting percentage cover to ordinal abundance based on biological community surveys at Pānia Reef (Sneddon and Crossett 2024).

Lyttelton Harbour and Fiordland (percentage cover)	Pānia Reef (ordinal abundance)	Description
0%	0	Absent
1–5%	1	Rare (1–2 individuals)
6–25%	2	Occasional (3–10 individuals)
26–50%	3	Common (> 10 individuals)
51–100%	4	Abundant (forms distinct zone)

Community composition of seaweed forests

Non-metric multi-dimensional scaling (nMDS) was performed using the Bray–Curtis dissimilarity index to investigate how the abundance of different functional seaweed groups varied across coastal locations in Aotearoa New Zealand. The dataset included median ordinal abundance (Table 3) for six functional groups – Phaeophyta (brown) canopy, Chlorophyta (green) subcanopy, Rhodophyta (red) subcanopy, Phaeophyta (brown) subcanopy, encrusting and turfing – across transects from Lyttelton Harbour (3–5 m and 6–8 m) and Pānia Reef. The analysis was performed in two dimensions, with 20 random starts to ensure a stable solution. The resulting ordination was rotated and centred for interpretability, and sites were plotted in ordination space to visualise differences in community composition across locations. Convex hulls were added to highlight patterns of community differentiation.

The percentage cover data from Fiordland were also analysed using nMDS with the Bray–Curtis dissimilarity index to assess differences in the abundance of different seaweed functional groups between the two fiord locations. The dataset included mean percentage cover of six functional groups across three data types (intertidal, transitional and subtidal) and two fiords (Doubtful Sound and Milford Sound), spanning depths from above the tide line to 16 m. The initial analysis was conducted with two dimensions, but the model was later adjusted to a three-dimensional ordination space ($k = 3$) due to a lack of a stable solution. The model was iterated up to 200 times to optimise the solution, with data retained on their original scale. Scores were extracted and visualised to highlight the differences in community composition between the two fiords, with hulls added to emphasise community distinctiveness across the sites.

To investigate change in seaweed community composition and abundance, we ran PERMANOVAs (PRIMER® v7.0.24) using seaweed functional groups from each region. All data were square-root transformed, and each PERMANOVA had 9,999 permutations and were based on Bray–Curtis similarity resemblance matrices of all samples (i.e. quadrats for Lyttelton Harbour and Fiordland data, and transects for Pānia Reef data). For the Bray–Curtis similarity matrices, a dummy variable of 0.01 was used so that double zero data were treated as 100% similar. The PERMANOVA design for Lyttelton Harbour had three factors: Site (fixed, 7 levels), Depth class (random, nested within Site, 2 levels: 4 m and 7 m), and Survey number (fixed, 11 levels). The PERMANOVA design for Pānia Reef had two factors: Site (fixed, 8 levels), and Survey number (fixed, 8 levels). The PERMANOVA design for Fiordland had four factors: Fiord (fixed, 2 levels: Milford and Doubtful Sounds), Site (random, nested in Fiord, 17 levels), Depth class (random, nested within Site, 4 levels: 0.5 m, 2–4 m, 7–10 m and 16 m), and Survey number (fixed, 12 levels). To further investigate which functional groups contributed most to compositional differences between locations, we conducted a SIMPER (similarity percentage) analysis. This analysis decomposed the Bray–Curtis dissimilarities into contributions from each functional group, identifying taxa that drove differences between pairs of locations. Permutation tests calculated significance values, and only groups with an $\alpha < 0.05$ were considered strong contributors to dissimilarity.

Sea surface temperature time-series

SST data were retrieved from NOAA's Coral Reef Watch Daily Global 5 km Satellite Sea Surface Temperature Anomaly product (Version 3.1, released 1 August 2018) to characterise temperature changes that might determine differences in seaweed abundances across sites and time. This dataset contains SST (°C) values and SST anomalies for a 0.05° satellite grid. The spatial extent of each site was cropped to specific bounding coordinates to prepare the SST data. In Lyttelton Harbour (Figure 6A), the extent was defined as the minimum enclosing rectangle between the area defined by the coordinates 43.7°S, 172.7°E and 43.5°S, 173.0°E. Mean SST and SST anomalies were calculated for each month from the year 2000 to 2024. Port of Napier's (Figure 6A) extent was set between 39.0°S, 176.0°E and 40.0°S, 177.0°E, with the same SST metrics calculated monthly for the same time range. For Fiordland (Figure 6B), the extent covered 47.5°S, 166.5°E to 34.5°S, 178.5°E, and annual anomalies were calculated as survey dates were not recorded at this site. Therefore, a monthly SST from 2006 to 2024 was created to capture all possible survey dates.

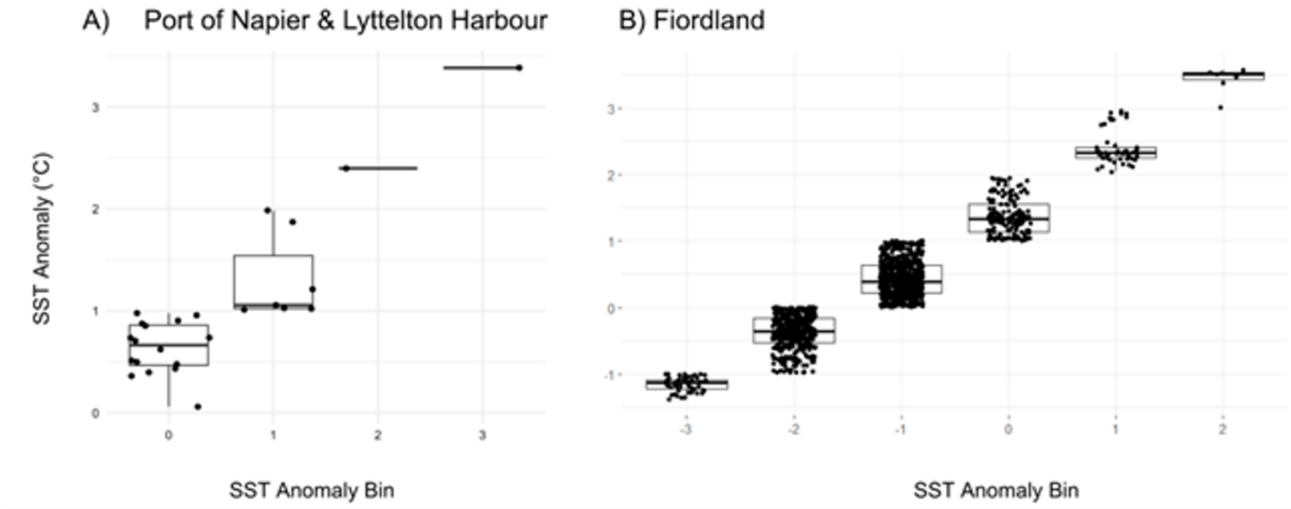

Figure 6. Sea surface temperature (SST) data, provided by NOAA Coral Reef Watch, were grouped into bins in preparation for statistical analyses based on the leading integer of the anomaly in °C. (A) SST anomaly data for all sites in the Port of Napier (Pānia Reef) and Lyttelton Harbour. (B) SST anomaly data for all sites in Fiordland.

2.3 Results

Community composition of seaweed forests

Most of the seaweed community data were zero-inflated, meaning a zero value was recorded for most seaweed taxa at individual sampling points when researchers were collecting data in the field. This was particularly true for transects surveyed in Lyttelton Harbour and most photo-quadrat surveys for intertidal and subtidal sites across Fiordland; this was likely because a higher diversity of seaweed species were observed in these areas, but many in low abundance. For example, 29 seaweed species or groups were identified in Lyttelton Harbour (both shallow and deep transects), 21 for intertidal and 23 for subtidal surveys in Fiordland, and 15 from surveys in Pānia Reef. However, in the shallow transects (3–5 m) at Lyttelton Harbour, encrusting seaweeds were present in nearly half of the surveys, while the rest of the groups and subgroups were present in less than a quarter (Figure 7A). In the deep transects (6–8 m) at Lyttelton Harbour, encrusting seaweeds were present in nearly one-third of the surveys, while the remaining groups and subgroups were present in less than a quarter (Figure 7B). Over a quarter of transects contained brown canopy and / or red subcanopy seaweed at Pānia Reef, while all other functional groups were present in fewer than a quarter of the surveys along this same reef (Figure 7C). In Fiordland, the brown canopy functional group was very low in abundance and only found in subtidal habitat, and at depths greater than 4 m for half of the sites across the two fiords (Figures 7D and 7E). All survey methods (i.e. intertidal, transitional and subtidal) in both fiords had relatively high (compared to Lyttelton Harbour and Pānia Reef) occurrences of encrusting, turfing and subcanopy red seaweeds, with subcanopy brown and green seaweed present across both fiords (Figures 7D and 7E).

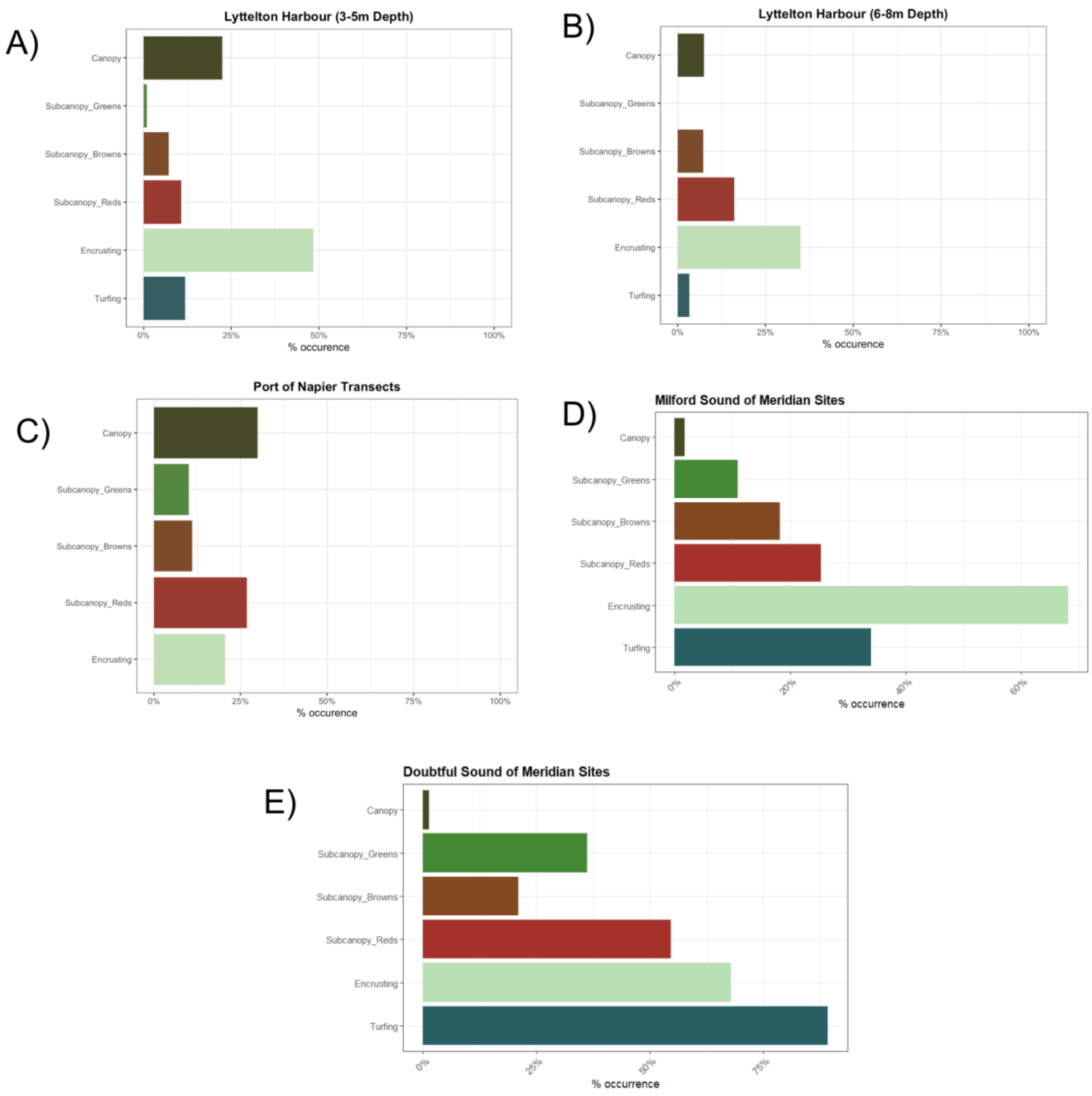

Figure 7. The percentage occurrence of functional groups and subgroups across all dive survey locations. (A) Data from shallow transects at Lyttelton Harbour (2016–24); (B) data from deep transects from Lyttelton Harbour (2016–24); (C) data from all transects from Pānia Reef (off Port of Napier: 2016–23); (D) data from intertidal, transitional and subtidal photo-quadrats from Milford Sound / Piopiotahi, Fiordland (with Meridian: 2007–24); (E) data from intertidal, transitional and subtidal photo-quadrats from Doubtful Sound / Pātea (with Meridian: 2006–24).

Non-metric multi-dimensional scaling (nMDS) for Pānia Reef and Lyttelton Harbour revealed distinct community compositions among the three sites (Figure 8). The axes represent variation in different functional groups (Table 2). Along axis 1, turfing and Chlorophyta or green subcanopy exhibit the highest scores and contribute most to the separation, with an inverse relationship where turfing groups increase as Chlorophyta subcanopy decreases (Figure 8). Axis 2 is primarily driven by differences in

Phaeophyta or brown subcanopy, followed by brown canopy and encrusting groups, which decline as Phaeophyta subcanopy increases (Figure 8).

A separate nMDS was conducted for all Fiordland sites and data types (Figure 9). There was a large degree of overlap of communities across all data types from both fiords in Fiordland (Figure 9). In the Fiordland nMDS plot, axis 1 is driven by an inverse relationship between floor (encrusting / turfing), and green and brown subcanopy seaweed. Axis 2 is driven by an inverse relationship between floor (encrusting / turfing) and subcanopy red seaweed. For example, Doubtful Sound had more subcanopy green seaweed and red seaweed, as well as more turfing seaweed species, than Milford Sound. In contrast, there were more subcanopy brown and encrusting seaweed species in Milford Sound compared to Doubtful Sound (Figures 7D and 7E).

Seaweed functional groups were significantly different among both reef sites (Pseudo-$F_{df=7}$ = 49.210, p = 0.001) and surveys (Pseudo-$F_{df=7}$ = 11.280, p = 0.001) at Pānia Reef. At Lyttelton Harbour, seaweed functional groups were not significantly different among sites (Pseudo-$F_{df=6}$ = 0.645, p = 0.737). However, seaweed functional groups were significantly different among both depth of reef (Pseudo-$F_{df=5}$ = 104.400, p = 0.001) and survey (Pseudo-$F_{df=10}$ = 2.030, p = 0.017). In Fiordland, seaweed functional groups were significantly different among fiords (Pseudo-$F_{df=1}$ = 3.476, p = 0.022), year of survey (Pseudo-$F_{df=11}$ = 5.300, p = 0.001), and depth of reef (Pseudo-$F_{df=27}$ = 55.100, p = 0.001), but were not significantly different based on site (Pseudo-$F_{df=15}$ = 1.281, p = 0.171). Two SIMPER analyses were conducted, and the first describes differences in average community composition between Lyttelton Harbour shallow transects, Lyttelton Harbour deep transects and Pānia Reef transects off the Port of Napier. The second compares average community composition with intertidal, transitional and subtidal data survey methods pooled from Milford and Doubtful Sounds in Fiordland. The deep transects at Lyttelton Harbour were characterised by a higher abundance of turfing species and lower canopy cover. In contrast, both Pānia Reef and shallow transects at Lyttelton Harbour contained canopy species, although Pānia Reef had fewer turfing species (Figures 7 and 8). Encrusting algae species were the highest contributors to differences between the Doubtful and Milford Sounds in the Fiordland sites. Additionally, brown subcanopy species were higher in Milford Sound, whereas turfing algae species had a high contribution to the community composition in Doubtful Sound. Brown canopy algae contributed minimally to the difference between the two fiords.

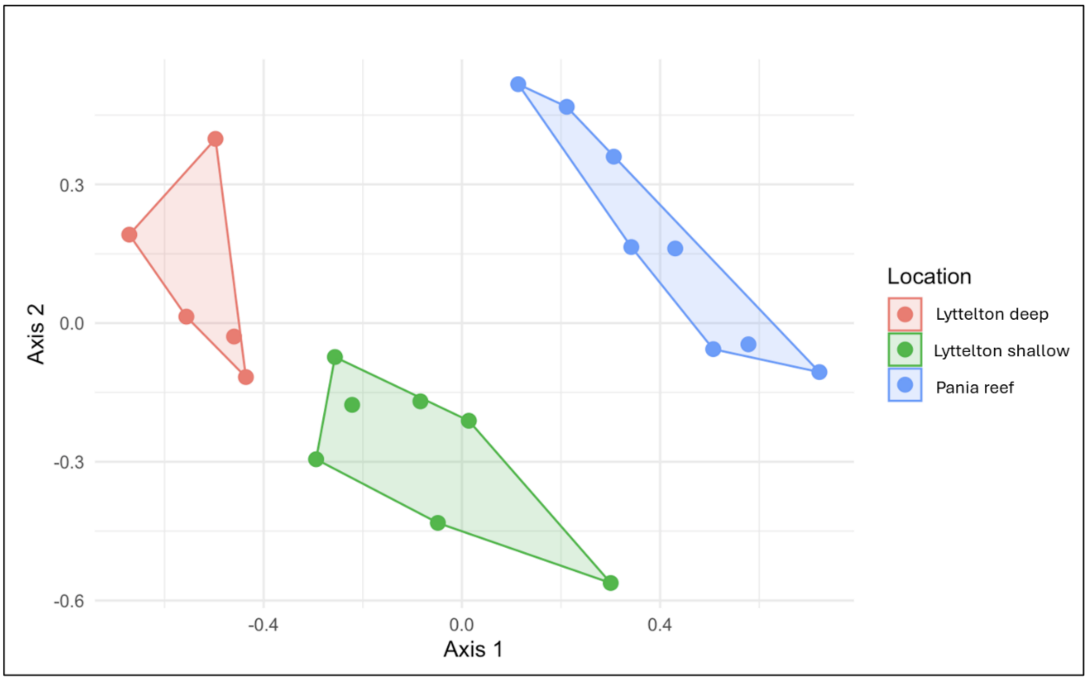

Figure 8. Non-metric multi-dimensional scaling (nMDS) creates a two-dimensional visualisation of the compositional differences for communities in three dive survey locations: Pānia Reef (2016–24), Lyttelton Harbour (deep transects, 6–8 m: 2016–24), and Lyttelton Harbour (shallow transects, 3–5 m: 2016–24).

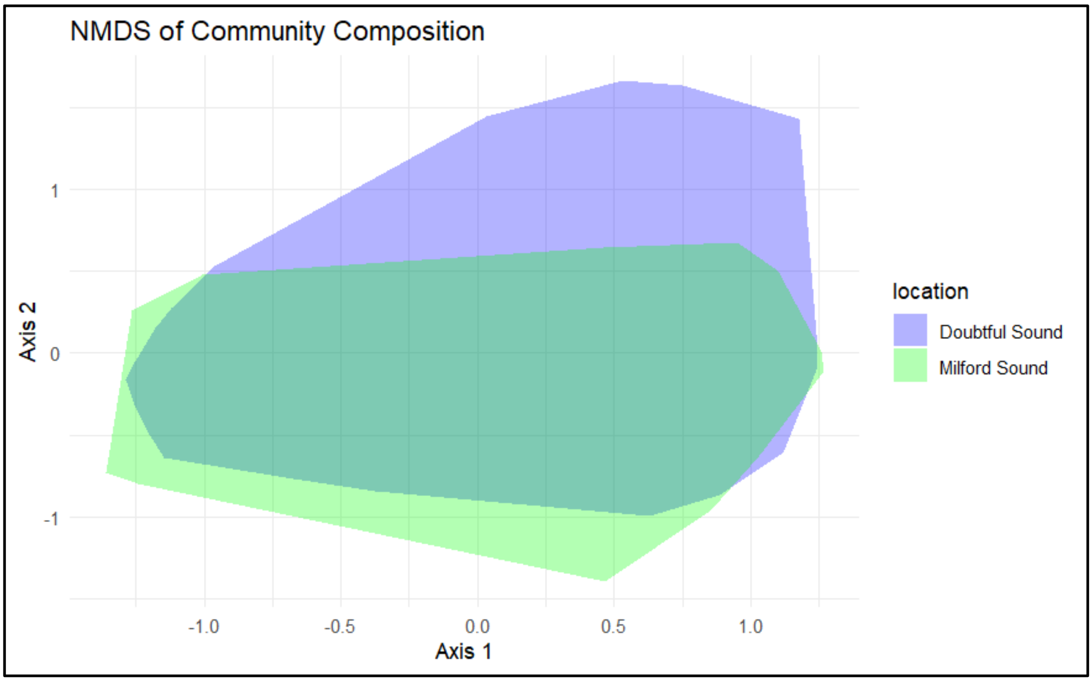

Figure 9. Non-metric multi-dimensional scaling (nMDS) creates a two-dimensional visualisation of the compositional differences for seaweed communities (all three data survey methods included: intertidal, transitional and subtidal) across the two fiords, Doubtful Sound / Pātea and Milford Sound / Piopiotahi, in Fiordland (data from 2006–24).

Pānia Reef

At Pānia Reef near the Port of Napier, abundance was recorded using an ordinal scale (Table 1) compared to percentage cover data recorded to estimate seaweed abundance in Lyttelton Harbour and Fiordland. Across all sites, there was a slight increase in abundance of subcanopy green and subcanopy brown species between 2016 and 2023 (Figure 13). Over this same period, the abundance of floor species remained stable, but there was a decline in brown canopy seaweed abundance and an increase in the abundance of subcanopy red seaweed. However, across all sites, and between November 2022 and October 2023, there was a notable decline in abundance of subcanopy red, subcanopy brown and canopy brown seaweed. There was also variability in changes of seaweed abundance from 2016 to 2023 among the different sites at Pānia Reef (Figure 13). For example, there were much higher sum of abundance scores of all seaweed at PR2 compared to PR5 at every sampling interval from 2016 to 2023. Also, at PR2, the sum of abundance scores of subcanopy green, brown and red seaweed all increased from 0.00, 3.00 (± 0.91 SE) and 1.20 (± 0.42 SE), respectively, in 2016 to 2.80 (± 0.29 SE), 4.60 (± 0.65 SE) and 7.60 (± 0.54 SE) in 2023. Whereas over this same period, there was very low or no subcanopy green seaweed found, and subcanopy brown seaweed abundances remained stable or slightly increased at all other sites (Figure 13). The abundance scores of subcanopy red seaweed had the greatest decline between 2016 and 2023 at PR4, from 6.00 (± 0.00 SE) to 4.00 (± 0.21 SE). The greatest decline of canopy brown seaweed abundance between 2016 to 2023 was at PR3, which recorded a change from 3.80 (± 0.20 SE) to 1.40 (± 0.43 SE).

Lyttleton Harbour

There were changes in seaweed functional groups, particularly a general increase in floor and canopy brown species, among the shallow transects at Lyttelton Harbour between 2016 and 2024 (Figure 10). However, change was site specific (Figure 11). For example, at site BP13, average percentage cover of floor species from 2016 to 2024 increased from 4.0% (± 0.96 SE) to 56.0% (± 4.54 SE). Additionally, the average percentage cover of canopy brown species from 2016 to 2024 increased from 26.3% (± 4.20 SE) to 45.6% (± 7.16 SE). In contrast, at site BP02, average percentage cover of floor species from 2016 to 2024 only increased from 47.5% (± 7.56 SE) to 56.8% (± 9.92 SE), and the average canopy brown percentage cover decreased from 12.6% (± 4.20 SE) to 9.7% (± 5.02 SE) over this same period. There were also notable declines in average percentage cover of both floor and canopy brown species at BP01, BP02 and BP14 between 2017 and 2018, with recovery from 2021 to 2024.

Between 2016 and 2024, the deep transects at Lyttelton Harbour had relatively low percentage cover (generally less than 5%) of all seaweed functional groups, except floor seaweed species, which had a general increase from around 20% to about 30% cover across all sites (Figure 10). Seaweed community composition was site specific, as was change in percentage cover among the seaweed functional groups over time (Figure 12). For example, at site BP02, there was a slight decline from 2016 to 2024 in average percentage cover of floor species from 6.3% (± 2.27 SE) to 1.9% (± 0.76 SE), while canopy brown species increases slightly from 0.0% to 0.4% (±0.38 SE) over this same period. However, at site BP14, average percentage cover of floor species increased from 30.9% (± 4.76 SE) in 2016 to 44.8% (± 5.82 SE) in 2024, and canopy brown species decreased from 15.4% (± 5.52 SE) to 0.0% over this same period.

Fiordland

Seaweed community composition and change of percentage cover over time in Fiordland was dependent on the depth of the rocky reef (i.e. intertidal [0.5 m: including transitional data, and subtidal from 2–16 m]; Figures 14 and 15; see Table 4 for average values, ± SE, for 2007, 2010 and 2024). For example, there was greater abundance or average percentage cover of subcanopy red, green and brown seaweed in the intertidal (including transitional data) and shallow subtidal (2–4 m) habitat compared to deeper (> 7 m) rocky reef habitat. There was also a decline in subcanopy red seaweed in the intertidal habitat in both fiords from 2007 (38.8% and 11.3% average cover in Doubtful and Milford Sounds, respectively) to 2024 (27.7% and 1.5% average percentage cover in Doubtful and Milford Sounds, respectively). Subcanopy red seaweed also declined across most depths, particularly from 2019 to 2024 (Figures 14 and 15). There was also a decline in subcanopy green seaweed in the intertidal habitats at both fiords from 2007 to 2024, decreasing from 24.4% to 11.5% in Doubtful Sound and 12.3% to 1.7% in Milford Sound. However, in contrast, floor seaweeds were most abundant between the 4 m and 10 m depth across both fiords, and there was generally greater abundance of floor seaweeds at 16 m depth compared to the intertidal habitats. There was also an increase in floor seaweeds in the intertidal habitat in both fiords from 2007 to 2024, with percentage cover increasing from 3.0% to 20.7% in Doubtful Sound and 0.6% to 21.0% in Milford Sound.

In Fiordland, composition of seaweed communities and change in abundance over time were also influenced by the fiord in which the seaweed communities grew (Figures 14 and 15; see Table 4 for average values, ± SE, for 2007, 2010 and 2024). There were generally more subcanopy red seaweeds in Doubtful Sound compared to Milford Sound, with more fluctuation in average percentage cover over the 2006–24 period (Figures 14 and 15). In contrast, there was generally more subcanopy brown seaweed in Milford Sound compared to Doubtful Sound, particularly in the intertidal (including transitional data) and shallow subtidal (2–4 m) habitat. There was very low abundance of brown canopy seaweed at both fiords, with a slight increase from 2007 to 2024. However, brown canopy seaweed was found in greater abundances at deeper sites in Doubtful Sound (4.3% at 16 m depth in 2024) than in Milford Sound (2.1% at 7–10 m depth in 2024).

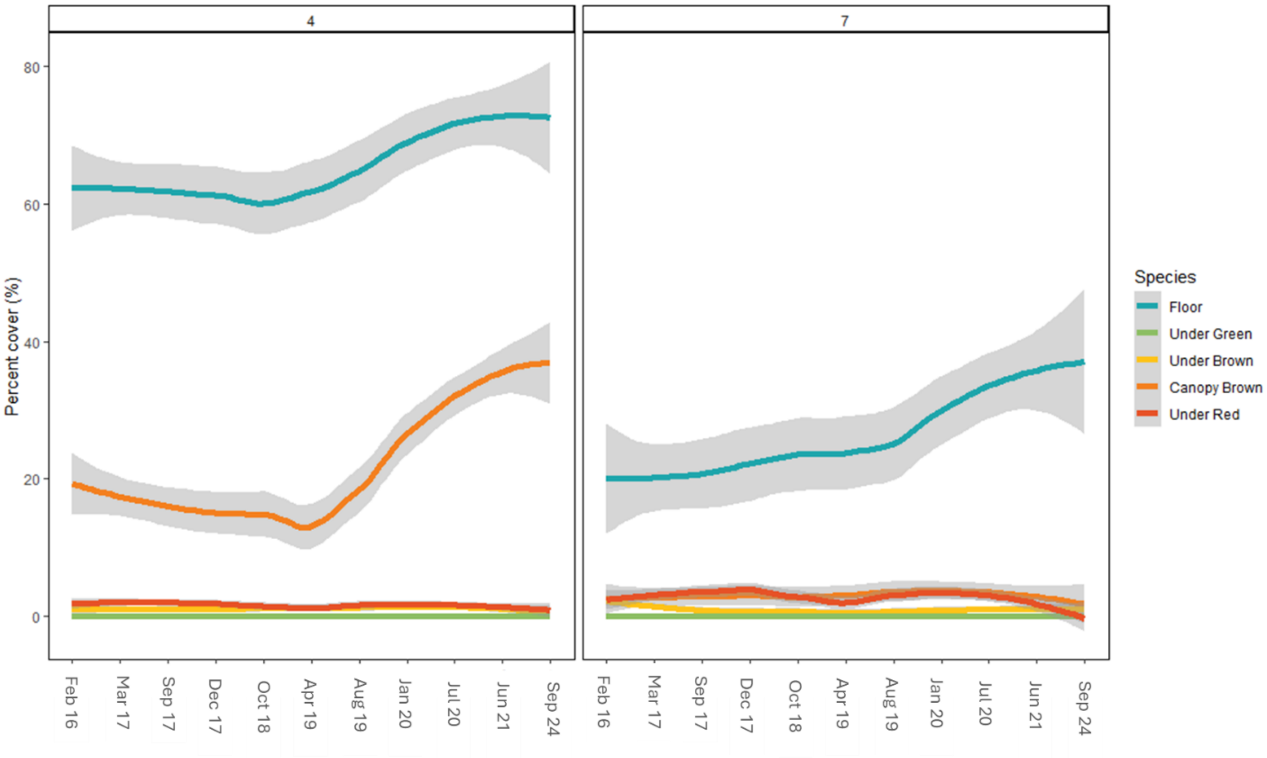

Figure 10. Time-series for seaweed functional groups in shallow transects (4: 3–5 m) and deep transects (7: 6–8m) whin Lyttelton Harbour from 2016–24. All sites are pooled for each panel. The coloured lines represent the different seaweed functional groups: floor seaweed (blue), subcanopy green seaweed (green), subcanopy brown seaweed (light brown), canopy brown seaweed (brown / orange) and subcanopy red seaweed (red). Lines and shadings represent means and their 95% confidence level, respectively, estimated using the LOESS method based on the geom_smooth function in R ('ggplot2' package; Wickham 2016).

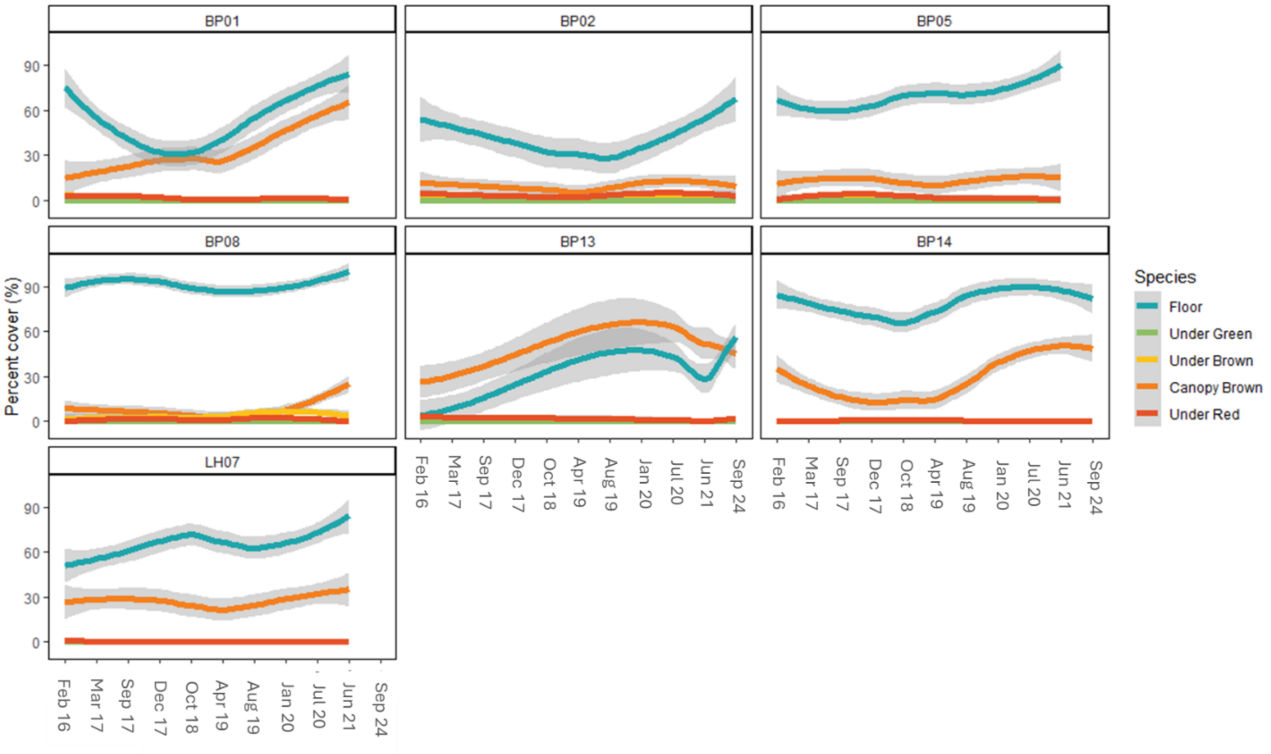

Figure 11. Time-series for seaweed functional groups in shallow transects (3–5 m) in Lyttelton Harbour from 2016–24. The coloured lines represent the different seaweed functional groups: floor seaweed (blue), subcanopy green seaweed (green), subcanopy brown seaweed (light brown), canopy brown seaweed (brown / orange) and subcanopy red seaweed (red). Lines and shadings represent means and their 95% confidence level estimated using the LOESS method based on the geom_smooth function in R ('ggplot2' package; Wickham 2016). Note that 2024 data only exist for sites BP02, BP13 and BP14, so caution must be taken when comparing line trajectory from 2021 at sites without 2024 data.

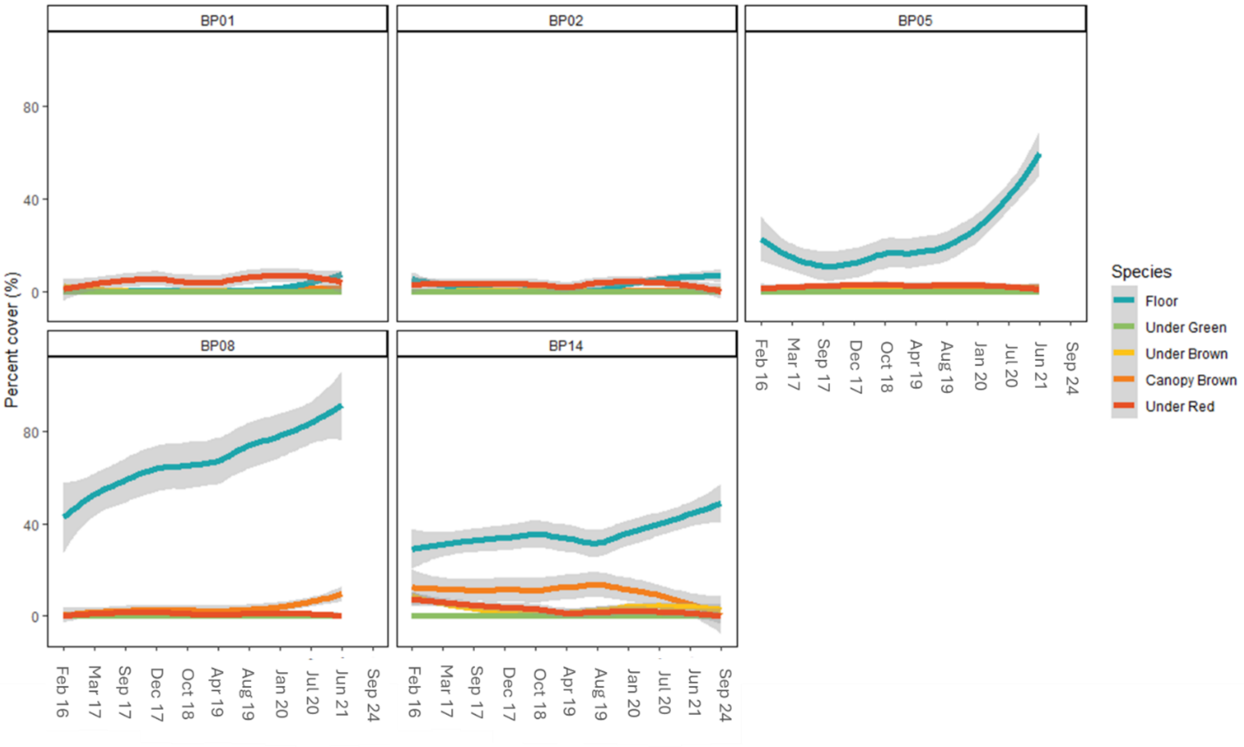

Figure 12. Time-series for seaweed functional groups in deep transects (6–8 m) in Lyttelton Harbour from 2016–24. The coloured lines represent the different seaweed functional groups: floor seaweed (blue), subcanopy green seaweed (green), subcanopy brown seaweed (light brown), canopy brown seaweed (brown / orange) and subcanopy red seaweed (red). Lines and shadings represent means and their 95% confidence level estimated using the LOESS method based on the geom_smooth function in R ('ggplot2' package; Wickham 2016). Note that 2024 data only exist for sites BP02 and BP14, so caution must be taken when comparing line trajectory from 2021 at sites without 2024 data.

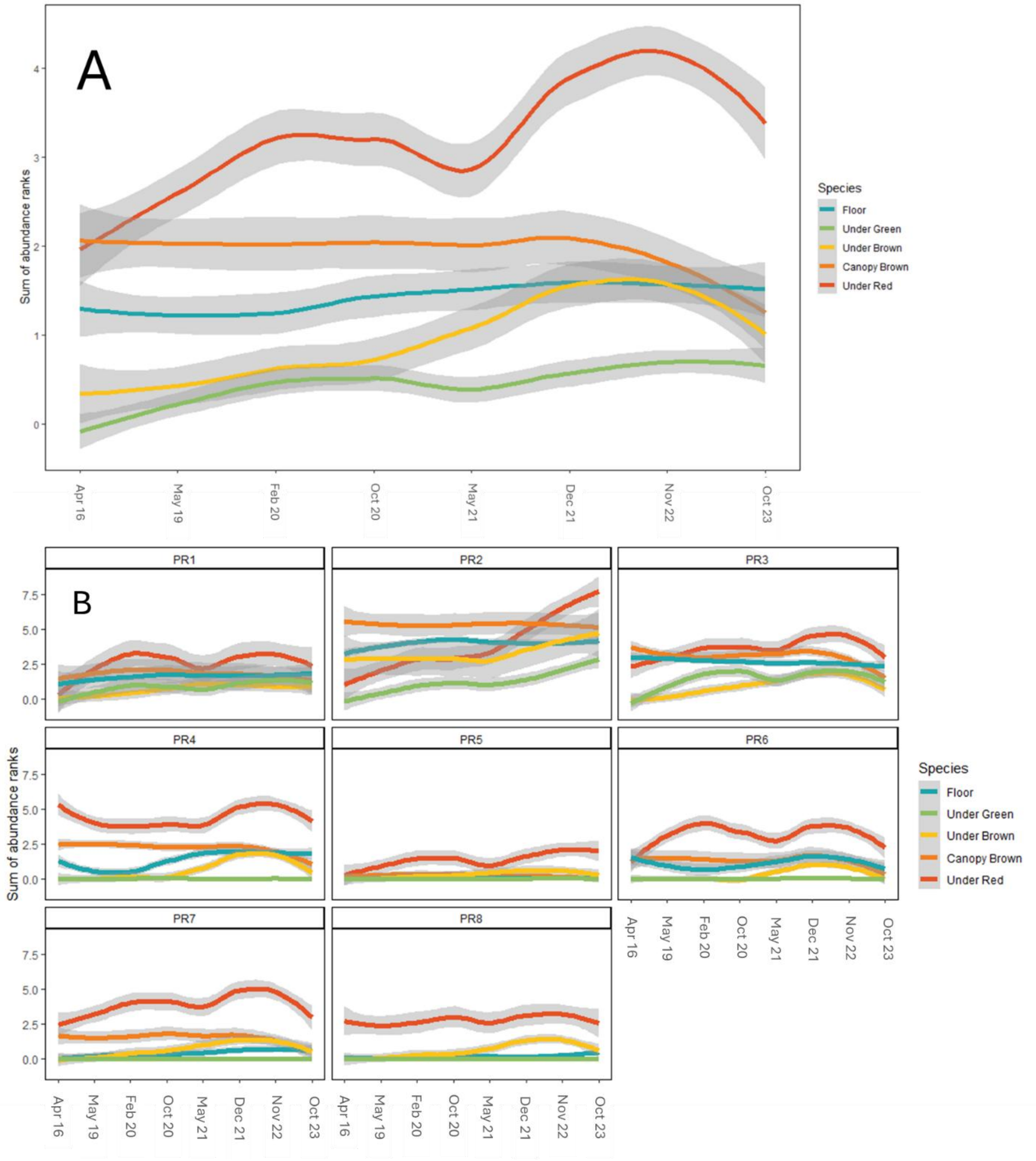

Figure 13. (A) Time-series for seaweed functional groups with all sites combined from data collected between 2016–23 at Pānia Reef near Port Napier. (B) Time-series for seaweed functional groups with sites separate from data collected between 2016–23 at Pānia Reef near Port Napier. For all panels, the coloured lines represent the different seaweed functional groups: floor seaweed (blue), subcanopy green seaweed (green), subcanopy brown seaweed (light brown), canopy brown seaweed (brown / orange) and subcanopy red seaweed (red). Note that the y-axis is in sum of abundance ranks based on the 0–4 rank scale used for collecting seaweed data at Pānia Reef. Possible maximum sum of abundance ranks differs for each functional group depending on how many seaweed taxa were identified over the project period in each functional group. The maximum for each group is: floor = 8; subcanopy green = 8; subcanopy brown = 20; canopy brown = 8; subcanopy red = 16. Lines and shadings represent means and their 95% confidence level estimated using the LOESS method based on the geom_smooth function in R ('ggplot2' package; Wickham 2016).

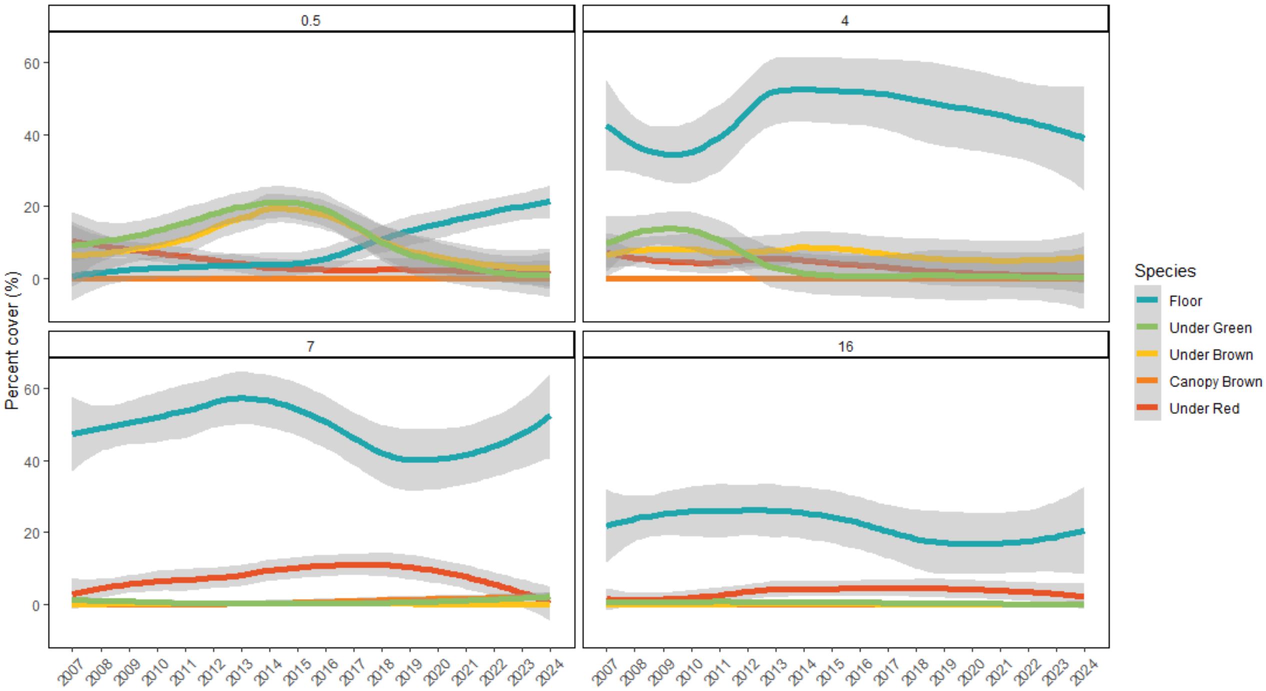

Figure 14. Time-series for seaweed functional groups averaged across all sites (1, 3, 4 for intertidal and subtidal data; and MN [Milford North] and MS [Milford South] for intertidal transition data) in Milford Sound / Piopiotahi – Fiordland. Depth class are 0.5: all intertidal and transition data; 4: 2 m and 4 m subtidal data combined; 7: 7 m and 10 m subtidal data combined; 16: subtidal data collected at 16 m. The coloured lines represent the different seaweed functional groups: floor seaweed (blue), subcanopy green seaweed (green), subcanopy brown seaweed (light brown), canopy brown seaweed (brown / orange) and subcanopy red seaweed (red). Lines and shadings represent means and their 95% confidence level estimated using the LOESS method based on the geom_smooth function in R ('ggplot2' package; Wickham 2016).

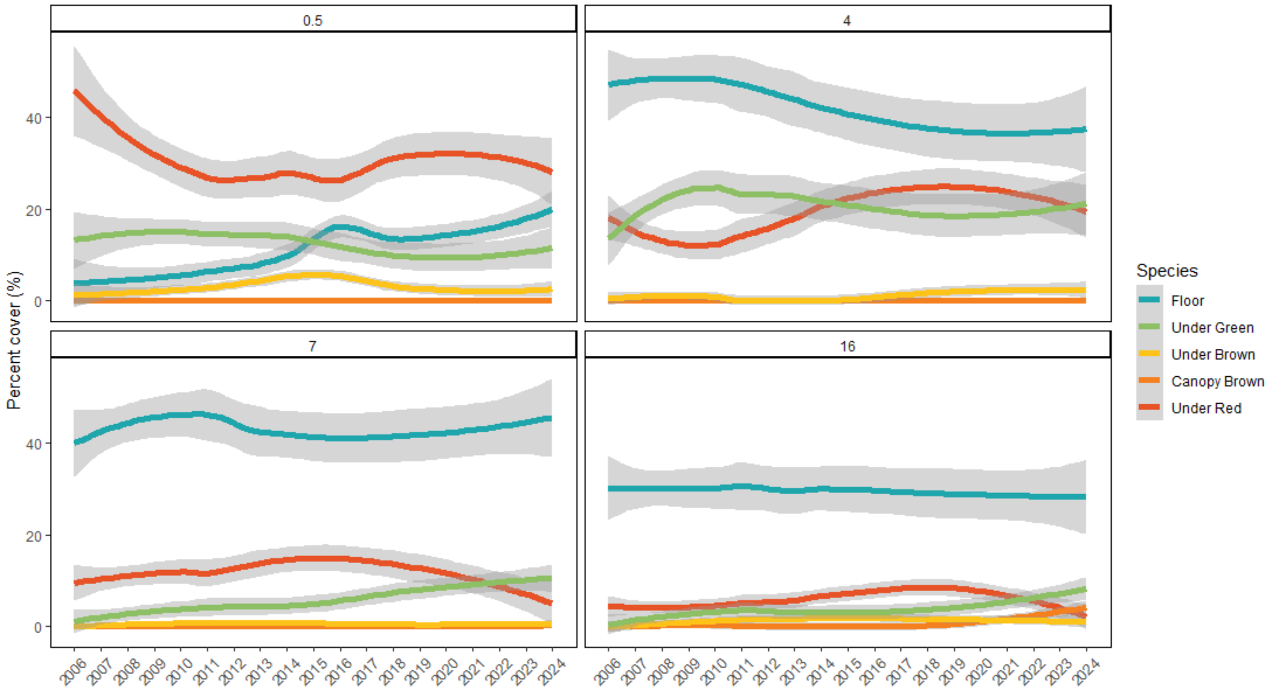

Figure 15. Time-series for seaweed functional groups averaged across all sites from 2006–24 (6, 9, 11, 13, 14, 15 for intertidal and subtidal data; CN, CS, FN, FS, GN, GS [representing various bays] for intertidal transition data) in Doubtful Sound / Pātea – Fiordland. Depth classes are 0.5: all intertidal and transitional data; 4: 2 m and 4 m subtidal data combined; 7: 7 m and 10 m subtidal data combined; 16: subtidal data collected at 16 m. The coloured lines represent the different seaweed functional groups: floor seaweed (blue), subcanopy green seaweed (green), subcanopy brown seaweed (light brown), canopy brown seaweed (brown / orange) and subcanopy red seaweed (red). Lines and shadings represent means and their 95% confidence level estimated using the LOESS method based on the geom_smooth function in R ('ggplot2' package; Wickham 2016).

Table 4. Average percentage cover for each seaweed functional group in Fiordland based on fiord (Doubtful Sound / Pātea vs. Milford Sound / Piopiotahi); Depth class 0.5: all intertidal and transition data; 4: 2 m and 4 m subtidal data combined; 7: 7 m and 10 m subtidal data combined; 16: subtidal data collected at 16 m; and year (2007, 2010 and 2024). ±1 SE are listed next to corresponding averages.

Fiord	Depth	Year	Floor	SE	Sub-Green	SE	Sub-Brown	SE	Sub-Red	SE	Canopy-Brown	SE
Doubtful	0.5	2007	2.96	1.03	24.35	7.43	0.37	0.29	38.80	7.48	0.00	0.00
Doubtful	0.5	2010	9.85	2.50	15.43	2.83	4.01	1.13	15.49	2.56	0.00	0.00
Doubtful	0.5	2024	20.65	2.42	11.47	1.99	2.67	0.83	27.68	3.49	0.00	0.00
Doubtful	4	2007	42.43	4.57	24.31	3.67	0.00	0.00	16.25	2.74	0.00	0.00
Doubtful	4	2010	47.92	4.86	24.53	3.94	0.42	0.26	11.82	2.27	0.00	0.00
Doubtful	4	2024	37.52	4.61	21.35	3.56	2.16	1.00	19.72	3.28	0.00	0.00
Doubtful	7	2007	41.50	4.36	1.83	1.17	0.00	0.00	10.08	2.67	0.00	0.00
Doubtful	7	2010	45.80	4.46	4.49	1.16	1.16	0.44	8.99	2.24	0.07	0.07
Doubtful	7	2024	45.46	4.66	10.28	2.32	0.71	0.29	5.18	1.61	0.21	0.12
Doubtful	16	2007	30.97	4.63	1.67	0.70	0.00	0.00	4.44	1.46	0.00	0.00
Doubtful	16	2010	28.75	4.17	5.00	1.65	1.11	0.52	4.03	1.24	0.14	0.14
Doubtful	16	2024	28.47	3.76	8.33	2.48	1.11	0.52	1.94	0.75	4.31	2.43
Milford	0.5	2007	0.63	0.44	12.29	4.84	6.04	2.85	11.25	4.19	0.00	0.00
Milford	0.5	2010	2.98	1.40	15.60	3.52	11.13	2.44	3.27	1.44	0.00	0.00
Milford	0.5	2024	20.95	4.52	1.67	0.70	3.15	1.42	1.49	1.19	0.00	0.00
Milford	4	2007	45.83	6.12	8.33	4.18	4.44	2.66	7.22	3.40	0.00	0.00
Milford	4	2010	33.75	7.88	15.14	7.04	10.28	4.54	4.58	2.09	0.00	0.00
Milford	4	2024	38.61	6.42	0.28	0.28	6.11	3.20	0.56	0.33	0.00	0.00
Milford	7	2007	46.25	5.10	0.83	0.50	0.00	0.00	1.67	0.67	0.00	0.00
Milford	7	2010	50.00	6.45	0.42	0.31	0.83	0.61	7.08	2.58	0.00	0.00
Milford	7	2024	53.61	5.71	2.22	1.39	0.00	0.00	0.14	0.14	2.08	1.80
Milford	16	2007	22.22	6.09	0.83	0.60	0.00	0.00	1.39	1.12	0.00	0.00
Milford	16	2010	28.33	6.24	1.11	0.63	0.00	0.00	2.50	1.93	0.00	0.00
Milford	16	2024	21.21	6.03	0.00	0.00	0.00	0.00	2.12	1.81	0.00	0.00

Sea surface temperature time-series

Aotearoa New Zealand experienced above-average SST anomalies and corresponding MHW nationwide during 2016–19 and 2022–23 (Straub et al. 2019; Thoral et al. 2022, and see dark red dots on Figure 16). Note that we did not specifically tests for MHWs, but the high SST anomalies found correspond to MHWs recorded from other studies. These SST anomalies were observed at Lyttelton Harbour and Port of Napier (Figure 17). The survey dates for Fiordland spanned 1 °C and 2 °C, as well as cold anomalies from −1 °C, −2 °C and −3 °C during the February months when photo surveys took place (Figure 18).

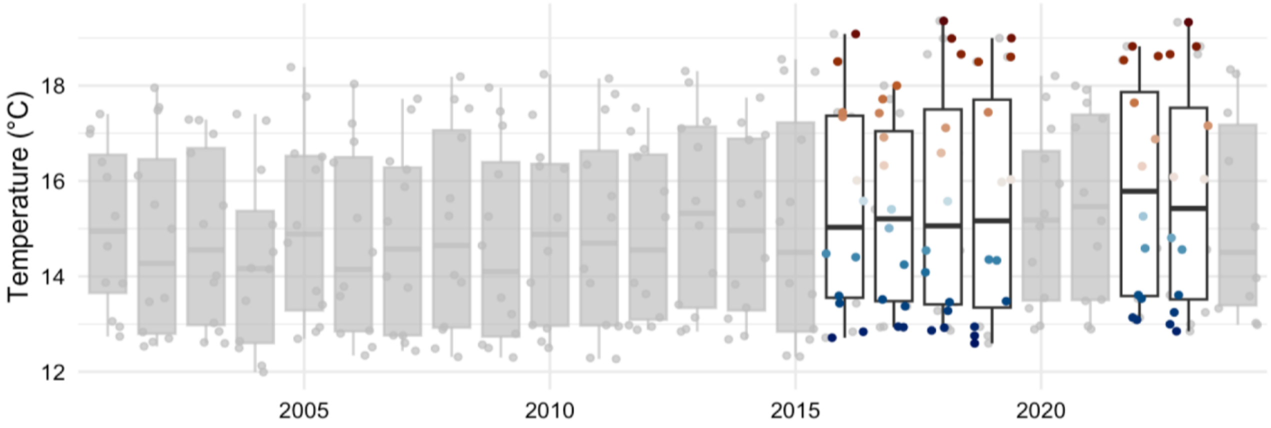

Figure 16. Annual average sea surface temperature (SST; in °C) distribution in Aotearoa New Zealand. Each point represents the monthly average SST across the extent of Aotearoa New Zealand's coastal waters. Darker coloured dots represent above or below average SST anomalies. Data provided by NOAA Coral Reef Watch Satellite Data for Aotearoa New Zealand between 2000–24.

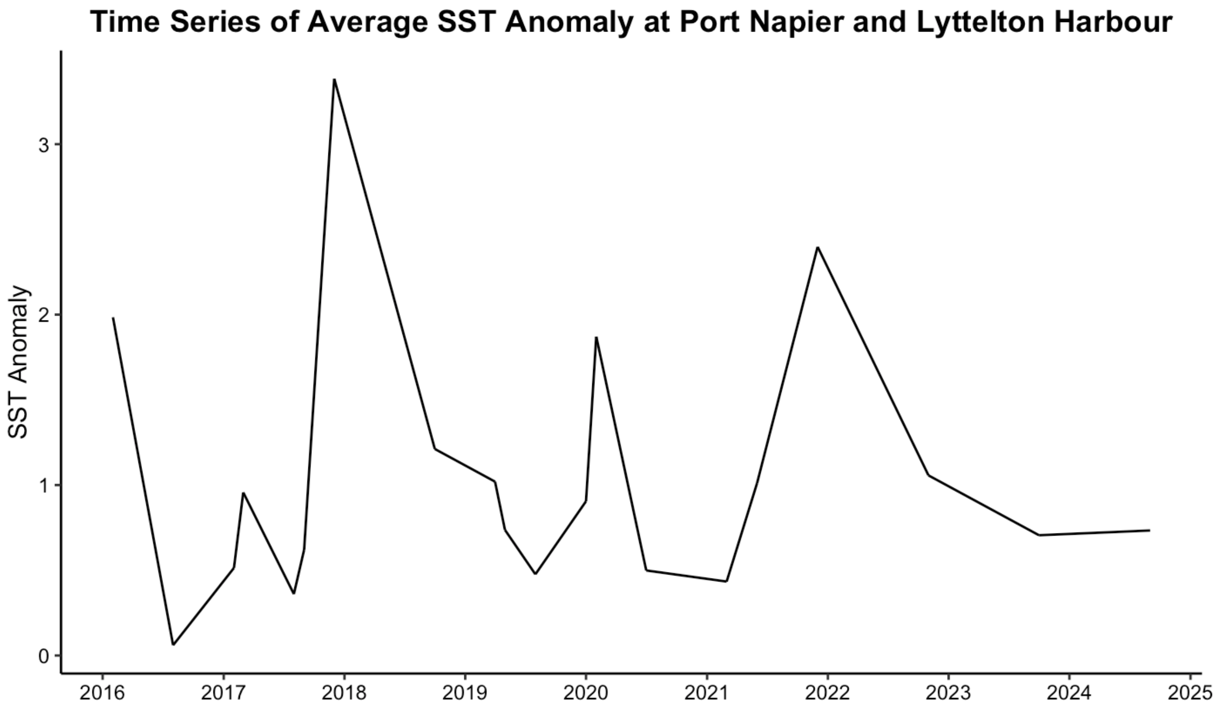

Figure 17. Sea surface temperature (SST) anomaly data from 2016 to 2025 retrieved from NOAA Coral Reef Watch. Average SST anomalies (°C) at Port of Napier (Pānia Reef) and Lyttelton Harbour show high SST anomalies between 2018 and 2022.

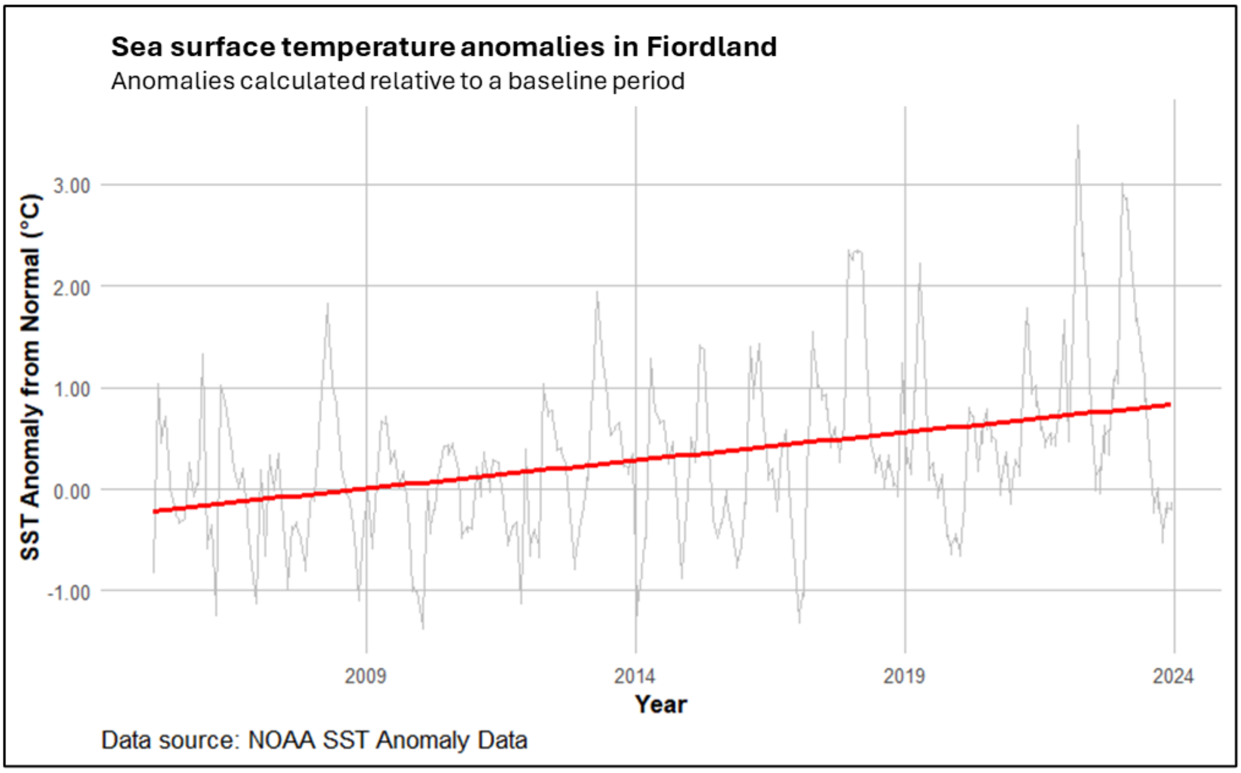

Figure 18. Sea surface temperature (SST) anomaly data provided by NOAA Coral Reef Watch. This data plot demonstrates average SST anomalies (°C) at Fiordland location (Milford Sound / Piopiotahi and Doubtful Sound / Pātea) from 2005 to 2024 with the historical average shown in red.

2.4 Discussion

From the early 2000s, there has been an increase in the number and strength of SST anomalies events in Aotearoa New Zealand (Thoral et al. 2022). Our data support this observation across the three study regions in Aotearoa New Zealand: Pānia Reef (Hawke Bay), Lyttelton Harbour (Canterbury) and Fiordland (Southland). Our study also highlights variations in the community composition of seaweed forests across these three coastal locations, with particular emphasis on variations in community composition based on the depths of the reef. Although we did not statistically test for relationships between SST anomalies and changes in seaweed communities, we observed trends in the data. For example, subcanopy brown and red seaweed at the shallow subtidal seaweed reefs in Lyttelton Harbour seemed to be more affected by SST anomalies than those recorded at greater depths in this same region. We suggest that this finding aligns with the recent literature (e.g. Straub et al. 2019; Schiel et al. 2021) and highlights the vulnerability of nearshore ecosystems to seawater warming events.

Thomsen et al. (2019) and Tait et al. (2019) reported low resilience of large brown canopy-forming seaweed (*Durvillaea* spp. and *Macrocystis pyrifera*, respectively) to MHW in the South Island of Aotearoa New Zealand. In contrast, our findings recorded an increase in abundance of brown canopy seaweed (*Carpophyllum* spp. and *Ecklonia radiata*) in the shallow subtidal sites at Lyttelton Harbour, particularly between 2019 and 2024. Both *Carpophyllum* spp. and *E. radiata* have larger latitudinal ranges than *Durvillaea* spp. and *M. pyrifera,* and because of this, likely have greater thresholds to warming seawater.

There is, generally, a negative correlation between subcanopy and the perennial canopy-forming species, which can grow high in the water column towards light and 'shade out' subcanopy species (Reed and Foster 1984; Connell 2005; Castorani et al. 2021). For example, the increase in canopy species at shallow-water communities at Lyttelton Harbour may have had a negative impact on subcanopy species.

Surveys at Pānia Reef, just offshore of the Port of Napier, did not show any clear trend in the effect of warming seawater and changes in seaweed communities. However, most of the reef surveyed at Pānia Reef was greater than 10 m and offshore, compared to the shallower coastal reefs surveyed at Lyttelton Harbour. The reef is notably deep with generally high turbidity in Hawke Bay; therefore, Pānia Reef has much lower abundance and diversity of seaweeds compared to Lyttelton Harbour and the reefs in Fiordland. The depth of Pānia Reef also likely buffered seaweed that does grow there against the impact of SST anomalies. However, there was evidence of the effect of extreme storm activity on the seaweed communities at Pānia Reef. In February 2023, Cyclone Gabrielle tore through the Hawke's Bay Region and directly across Pānia Reef, causing incredible damage to Napier and the wider area.[6] The effects of this extreme weather event are seen in the notable decline in abundance of subcanopy red, subcanopy brown and canopy brown seaweed at all sites between the November 2022 and October 2023 surveys. The impact of this one extreme weather event may have confounded the relationship between SST anomalies and seaweed functional groups at Pānia Reef.

The location of rocky reefs (i.e. Milford Sound vs. Doubtful Sound) and the depth of the reef both have significant influences on seaweed community composition in Fiordland. It is likely that location and depths of reefs also influence the resilience of seaweed communities to warming seawater temperatures. For example, from 2007 to 2024, there was an increasing trend of longer and stronger SST anomalies in Fiordland (Figure 18; Crossett et al. 2024) and a decline of red subcanopy seaweed in the intertidal and shallow subtidal zone across both fiords. Specifically, there was near total loss of the red seaweed, *Apophlaea lyallii,* from the intertidal zone in Milford Sound between 2019 and 2024 (Crossett et al. 2024). However, we also noted that the abundance of subcanopy seaweed was the lowest at 16 m across both Milford and Doubtful Sound throughout the study period. There may be less influence of warming seawater at greater depths in Fiordland, but it may have more impact on other reef organisms, such as sponges[7] or black coral[8]. This reinforces the need to account for depth-related habitat constraints in seaweed forest (as well as other associated important foundational taxa) management strategies and that any changes in seaweed community abundance or diversity will be region-specific. Moreover, there are many stressors to seaweed communities that are beyond and associated with SST anomalies or rising seawater temperatures (Straub et al. 2019; Thomsen et al. 2019; Filbee-Dexter et al. 2020), such as coastal sedimentation (Airoldi 2003; Tait et al. 2021) and overfishing (Ling et al. 2015; Miller and Shears 2023), which can aggravate the impact of the rising temperatures. Seaweed communities may be able to resist one or two disturbance events, but multiple and accumulating stressors will likely lead to tipping-point events impacting these important coastal habitats. However, if an ecosystem is already in a 'well-buffered', environmentally favourable and stable state, it is likely to have higher resilience to unforeseen perturbations. Thus, any action that will benefit the current, desired state will likely prove advantageous against future disturbance events.

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[6] Cyclone Gabrielle - Wikipedia

[7] Impact of 'largest' bleaching event on Fiordland sea sponges revealed

[8] Our Changing World: Fiordland's underwater world | RNZ News

3. Engagement with Māori

Tangata whenua of Aotearoa New Zealand are deeply connected to the environment, and many value holistic, nature-derived approaches to ecological management. Mātauranga Māori (Māori knowledge), which is shaped by exercising kaitiakitanga (environmental guardianship), mauri (life force), mana (spiritual power) and tapu (spiritual restrictions), guides their environmental practices (Love 2018; Taikato 2021). Māori participation in ecosystem management is required in Aotearoa New Zealand, reinforced by laws such as the Marine and Coastal Area (Takutai Moana) Act 2011, which integrates Mātauranga Māori and recognises that Māori have rights to use resources in specific ways (Mackill and Rennie 2011). Additionally, the Fisheries (Kaimoana Customary Fishing) Regulations 1998 and Fisheries (South Island Customary Fishing) Regulations 1999 reinforce tangata whenua having mana whenua and mana moana to establish reserves for sustainable non-commercial fishing.

Legislation and regulations are necessary due to the shortcomings of Aotearoa New Zealand's original foundational document, the Treaty of Waitangi / Te Tiriti o Waitangi, first signed on 6 February 1840 (Stokes 1992). The Treaty has both an English and a Māori version, which has led to conflicting interpretations (Kawharu 1989, Stokes 1992). The English version asserts sovereignty, while the Māori text suggests governance rights interpreted as a partnership. However, debate remains about the true intent and meaning of the Treaty.

McCarthy et al. (2014) illustrated how Māori perspectives can inform coastal management project objectives. Researchers assessed the decline in kaimoana (seafood) by engaging with 62 Ngāi Tahu members (the largest iwi of the South Island). Interviewees cited overfishing and changes in fisheries management as key factors in environmental degradation. The depletion of taonga (revered species) such as pāua (abalone) and other seafood is not simply a lost food resource but also a loss of cultural identity, tradition and community cohesion (McCarthy et al. 2014). The integration the generational knowledge of mana whenua and kaitiakitanga, through mātauranga Māori is important for modern ecological practices due to the long history of Indigenous people and their connection place in Aotearoa New Zealand. Through the integration of mātauranga Māori and Western science, coastal managers, kaitiaki and scientists can forge a path, together, towards sustainable environmental stewardship and ensure the resilience and vitality of Aotearoa New Zealand's precious marine ecosystems for future generations.

Objectives

1. Gather information through engagement and an online survey to understand if iwi / hapū kaitiaki (guardians) and tangata whenua (Indigenous peoples of Aotearoa New Zealand) living in Te Tauihu Te-Waka-a-Māui (the top of the South Island) have experienced a change in rimurimu (seaweed) forest ecosystems, and if a change has occurred, what are the impacts.
2. Determine to what extent this issue overlaps with the cultural identity for Māori in Te Tauihu.

Rationale

Many tangata whenua living in Aotearoa New Zealand have an intimate spiritual relationship with rimurimu (seaweed) and many of the living organisms in coastal and marine habitats. Specifically, many taonga species live within seaweed forests, such as pāua and kina (sea urchins). Seaweed forests are also crucial to Māori culture through the provision of kaimoana and the associated economies, such as fishing. Moreover, many tangata whenua take on the responsibility of kaitiaki, acting as stewards of seaweed forests and local coastal ecosystems for hundreds of years. Understanding the opinions, experiences and values of tangata whenua concerning the environment is essential to Aotearoa New Zealand's political system. The cultural understandings learned from our surveys will be paired with the natural science portion of this research project to guide policy recommendations.

3.1 Methods

We documented the opinions, experiences and values of tangata whenua in Te Tauihu using a survey questionnaire that focused on personal experiences, policy, natural resource management and the natural environment. The surveys were conducted using the Qualtrics survey tool. Survey participants were asked to set aside approximately 5–10 minutes to complete the survey and answer 18 questions (including cultural identity, economics, ecology and demographics). No prior preparation was necessary since participants' responses were based on their everyday activities, direct experience and personal knowledge of impacts on the environment in Aotearoa New Zealand. Confidentiality was preserved, as no information identifying participants is retained beyond the University of California Santa Barbara's Institutional Review Board (IRB) timeline, and all data are identified only with a code number. Data are stored on a secure electronic server and will be destroyed within the IRB-required time frame. No incentives were provided for survey participants. Participants could give their consent at the start of the survey, and they were informed that their participation involved answering a survey of opinions and experiences of mana whenua related to the environment. Participants could withdraw their consent at any time during or after the survey The subject population was contacted through Cawthron's Māori and Indigenous Research & Development Team, Te Kāhui Āio. The IRB has approved all methods of this study, and human ethics research was approved through Cawthron's robust human ethics research committee, which includes an external reviewer.

Cawthron distributed the survey to Māori stakeholders and iwi leaders from Te Tauihu, as well as Pou Taiao (environmental) managers and iwi whānau who Cawthron knew spent time in or on te moana (ocean). The online survey was sent out three times between December 2024 and February 2025 to a group with 31 members. All members were also asked to forward the online survey to other interested people. As of 10 February 2025, when the online survey was closed, there were 19 responses. Although 19 responses were recorded, not all respondents answered every question. Once the survey was closed, we interpreted the results qualitatively through the Qualtrics interface and in Microsoft Excel®.

In-person hui

On 17 September 2024, Cawthron organised a hui with a number of Māori community members that was hosted by Te Ātiawa O Te Waka-A-Māui Trust at Te Ara Kaimoana, Waikawa Marina, Waitohi

(Picton). A hui in Māori culture calls together a group for a specific purpose. Although this particular hui was not analysed for this project, the topics discussed informed many of the survey questions. A major theme that influenced the creation of at least one survey question was the impact of kina on seaweed forests and the role kina plays as an ecological and cultural component in reef communities. One hui participant mentioned that kina often receives too much blame for negative impacts on seaweed forests. The participant stated that since seaweed and kina have existed together for thousands of years, the problem is likely very complex. However, there is evidence that kina management can mitigate degraded seaweed habitats (Miller and Shears 2023; Miller et al. 2024), and that an over-abundance of kina can cause significant decline of seaweed forests through over-grazing (Ling et al. 2015). Although kina are native herbivores and grazers that have always lived in seaweed forest communities, one reason for their over-abundance may be a decrease in predators and the collapse of important trophic cascades (Ling et al. 2015). For example, overfishing predators such as kōura (crayfish) and snapper may result in an increase in kina abundance. There was also discussion on potential water quality issues that may affect seaweed forests, as well as the desire to be included in seaweed forest restoration activities.

3.2 Results

In total, we received 19 survey responses. Due to low number of responses, we were not able to statistically analyse the results, but the data were put into graphs and visualised for qualitative analysis. Based on complete responses, most respondents (n = 8) answered that they had low te reo Māori fluency. Only three responded that they had medium-level fluency, one answered high fluency and one answered very high. None of the respondents answered that they had very low or no fluency.

Most respondents (n = 16) answered that they thought land-use practices could negatively impact seaweed forests, while one respondent was unsure (Figure 20). Most respondents (n = 9) answered that they had not seen an increase in kina abundance. Four respondents indicated that they had seen an increase, and two were unsure (Figure 19).

Most respondents also had a high level of familiarity with the concept of taonga species (n = 9; Figure 20). Specifically, four had ‘very high familiarity’, and five had ‘some familiarity’ (Figure 20). For the question on the importance of preserving taonga species, all respondents selected ‘moderate’ to ‘very high importance’, with the majority (n = 13) selecting ‘very high importance’ (Figure 20). Most respondents felt that they were highly familiar with the Treaty of Waitangi (n = 12), while only one was ‘very highly familiar’ and four were ‘moderately familiar’ (Figure 20).

When asked about the negative impacts of commercial fishing, the majority of respondents selected ‘high’ impact (n = 8). Most respondents expected a ‘moderate positive’ impact on their community if seaweed aquaculture was established (n = 7), with the second most common response being ‘high positive’ impact (n = 4). However, ‘very high’, ‘very low’, and ‘prefer not to answer’ all had two responses each (Figure 21). All respondents were either ‘moderately’, ‘highly’, or ‘very highly’ concerned about climate change (Figure 21).

Seventeen of the 19 survey respondents had participated in kaitiakitanga (Figure 22). Fifteen had participated in mahinga kai, and 10 in karengo harvesting. Only four had participated in muttonbirding and only one had participated in making or using pōhā bags. All respondents selected at least one activity (Figure 22).

Lastly, we asked participants if they would volunteer their time towards seaweed restoration. The largest number of selected responses was ‘1 to 5’ days per year (n = 4), but the remainder varied in number (Figure 23). ‘Prefer not to answer’ was chosen by three of the respondents, as was ‘16 to 20’ hours. One person answered ‘none’, i.e. they would not volunteer their time (Figure 23).

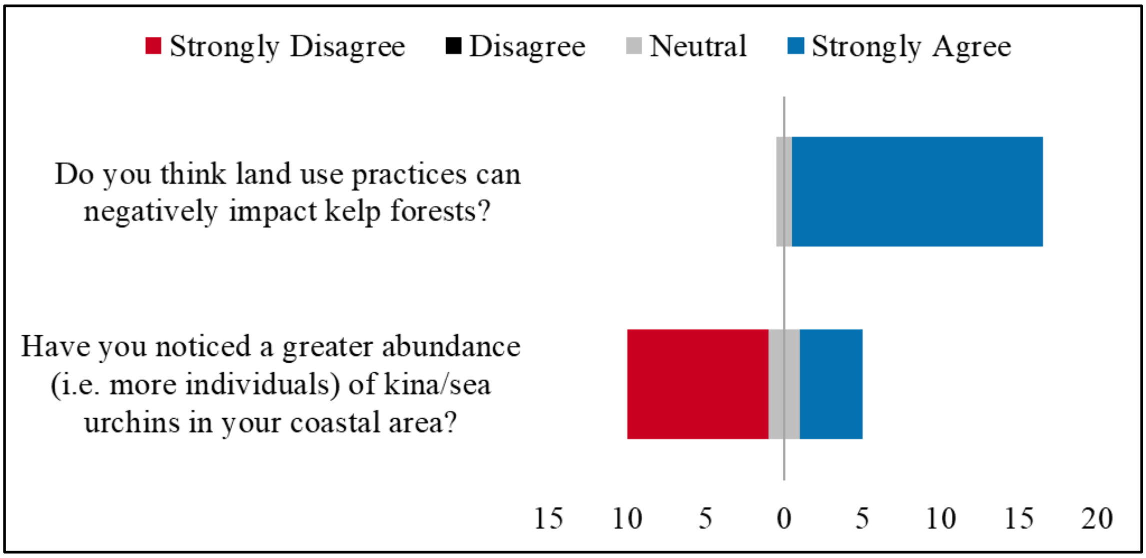

Figure 19. Responses to two separate questions regarding kina and land-use impacts. This figure shows the number of responses for each question, with disagreement on the left and agreement on the right.

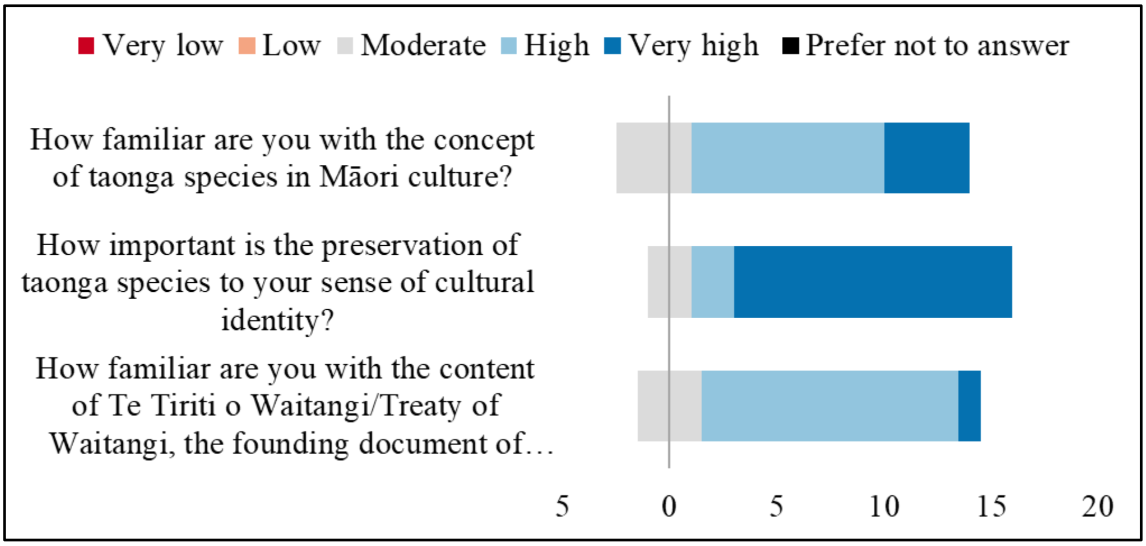

Figure 20. Importance of taonga and Treaty of Waitangi to cultural identity. This figure shows the number of responses for each question, with lower familiarity on the left and higher familiarity on the right.

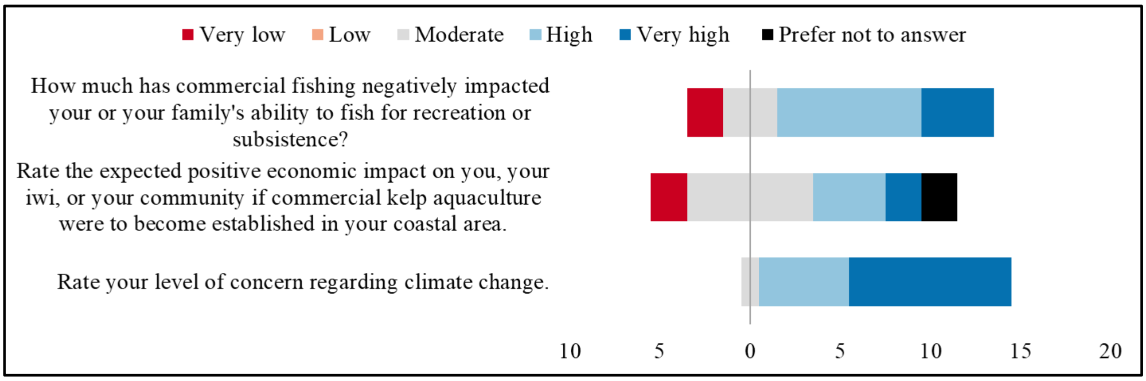

Figure 21. Concern surrounding climate change, kelp aquaculture and fishing. This figure shows the number of responses for each question, with low levels on the left and high levels on the right.

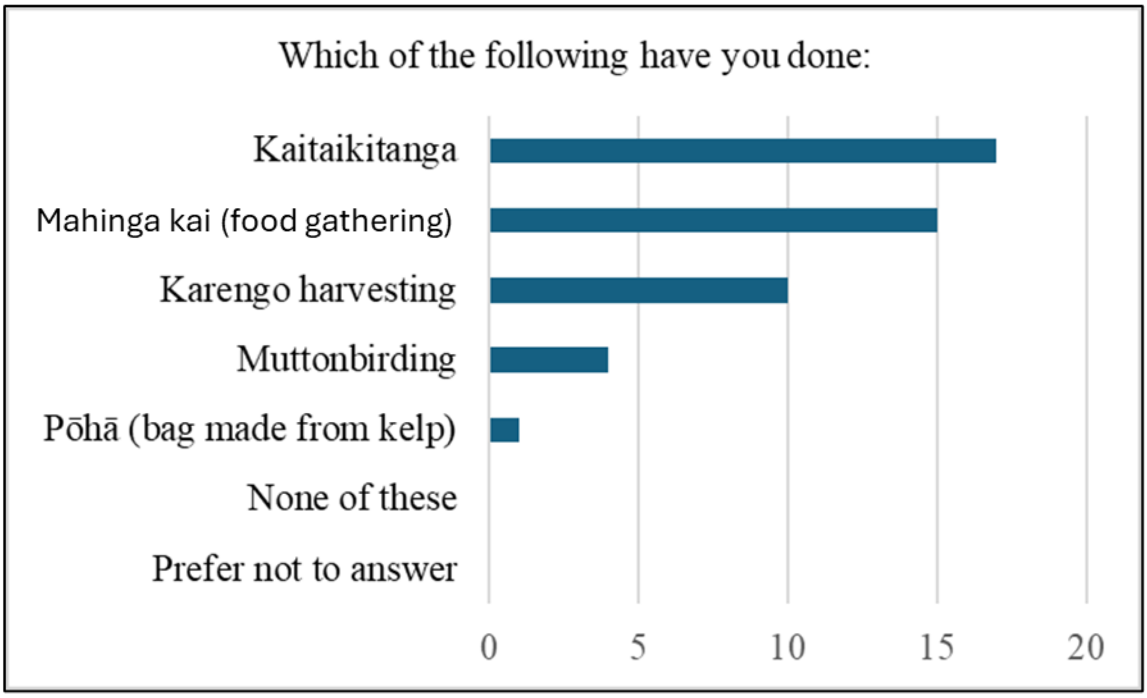

Figure 22. Participation in Māori traditional activities. This figure shows the number of activities each respondent had participated in. Respondents could multiple activities.

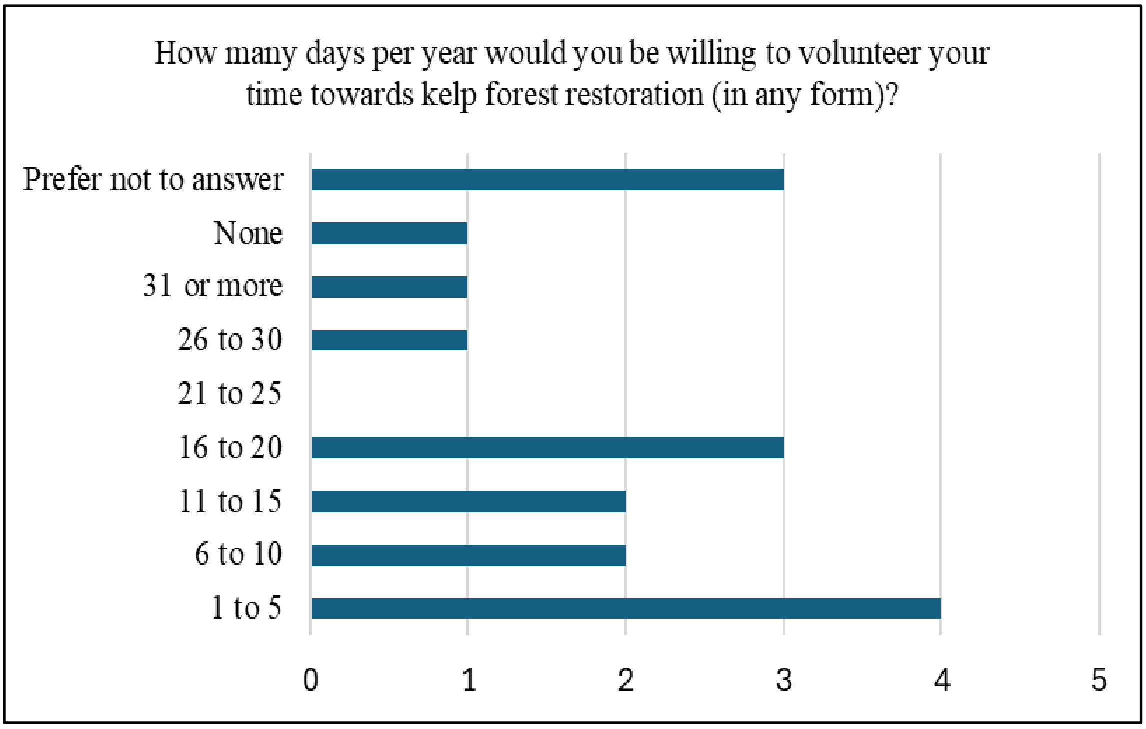

Figure 23. Volunteering time towards kelp restoration. This figure shows the number of days each respondent would be willing to participate in per year.

3.3 Discussion

The majority of respondents seemed to be highly engaged with Māori culture and to value the environment. Most were concerned or highly concerned about climate change. All respondents stated that they value taonga, and gave this question a rating of 'moderate' to 'very high' importance, with the majority selecting 'very high'. When asked how much of a negative impact commercial fishing has on their family's ability to fish, the majority of respondents stated that it has a 'high' or 'very high' negative impact. However, most participants responded that commercial seaweed aquaculture would have a 'moderate' to 'very high' positive impact. This seems to imply that community members are optimistic that seaweed aquaculture could provide benefits if they are involved early on. An additional surprising result is that although increasing numbers of kina are often blamed for decreasing seaweed forests, the respondents had not observed increased kina levels. The respondents also suggested many people who would be good contacts for future work or projects.

Lastly, most respondents answered that they thought land-use practices have negatively impacted seaweed forests. This is an interesting result, and it is encouraging to see the connection of land and sea being clearly articulated in this survey. In addition, studies have shown evidence of poor land management contributing to coastal sedimentation and associated degradation of coastal ecosystems (Krumhansl et al. 2016; Urlich and Handley 2020). Seaweed forests are particularly sensitive to coastal sedimentation because fine sediment can smoother seaweed and reduce their photosynthetic efficiency (Tait et al. 2021; Wing et al. 2022; Crossett et al. 2023). This also highlights the high complexity (brought up in the hui) around factors contributing to rimurimu change and the importance of engaging with the whole community to ensure the current and future management of this critical but declining habitat.

It is also essential to understand the context of questionnaires and how participants may interpret a survey question. For example, Figure 28 shows answers that express the participants' concerns about climate change, seaweed aquaculture and commercial fishing. Commercial fishing can come in many different forms, and in Aotearoa New Zealand, this includes trawling (generally for finfish species), and diving for pāua and kina. It is likely that most participants considered commercial fishing to be the taking of finfish, but this assumption cannot be confirmed. We suggest a future survey could seek further information on the impact of specific fisheries on people and places. Furthermore, it is important to keep clauses consistent in questions, and this principle will be followed for future surveys. For example, in Figure 21, participants were asked if seaweed aquaculture would have a 'positive' impact, while in the next question, participants were asked if they had experienced a 'negative' impact from commercial fishing. Figure 19 also includes wording that may have caused confusion: two questions that used the format 'Agree' or 'Disagree' may have been better phrased with 'Yes' or 'No'. After considering the results, and this study in general, it may have been more appropriate to present a statement such as 'Land-use practices have negatively impacted the seaweed forest' with the option to 'Agree' or 'Disagree'. It is unclear if these inconsistencies affected the results; however, we will endeavour to improve the format of future surveys.

4. Conclusions and recommendations

The loss of seaweed forest worldwide is alarming, and it is clear that these important habitats in Aotearoa New Zealand are not immune to the effects of a changing climate and other anthropogenic impacts. However, we cannot quantify change without baseline data, and the long-term datasets investigated in this project represent a unique view of seaweed communities over an extended time. Here, we provide evidence that seaweed forest composition and abundance are both influenced by region and local habitat, including depth of rocky reefs. For example, subcanopy red seaweed made up the greatest proportion of the seaweed community at Pānia Reef. In comparison, Lyttelton Harbour had greater proportions of canopy-forming and encrusting floor seaweed. However, from 2016 to 2023, there was a general decline of canopy-forming seaweed at Pānia Reef, with an increase in red subcanopy seaweed. Over this same period in Lyttelton Harbour, there was a general increase in canopy-forming seaweed and a decline in red subcanopy seaweed. In Fiordland sites, subcanopy red seaweed made up a greater portion of the intertidal and shallow subtidal seaweed communities in Doubtful Sound, compared to subcanopy brown and green seaweed contributing greater proportions in these same habitats in Milford Sound. However, at both fiords, floor species, such as encrusting and turfing seaweed, had greater contributions to seaweed communities as depth increased. There was also a general decline in red subcanopy seaweed in the intertidal and shallow subtidal habitats across both fiords from 2006 to 2024.

We did not statistically test the effects of SST anomalies on seaweed communities across all three regions over the study period because it was outside of the scope of this exploratory study. However, we observed trends suggesting negative relationships between SST anomalies and seaweed community composition, particularly for subcanopy seaweed. There is evidence that suggests negative impacts of SST anomalies on large brown canopy-forming species, such as *Durvillaea* spp. (Thomsen et al. 2019) and *Marcocystis pyrifera* (Tait et al. 2021). Understanding how subcanopy seaweeds are affected will help managers identify communities that may be particularly vulnerable to heatwaves and ongoing warming. For example, at all three study regions surveyed for this report, the majority of large brown canopy-forming seaweed were *Ecklonia radiata* and *Carpophyllum* spp., which have large latitude ranges (Wernberg et al. 2019), and are likely more resilient to thermal stress. And in the case of Fiordland, abundance of canopy-forming seaweeds was initially very low based on site selection in 2006–07. Subcanopy seaweeds play a crucial role in seaweed communities (Shear and Babcock 2007; Castorani et al. 2021), and they are critical food sources for many highly prized fishery and taonga species (e.g. pāua;[9] White and White 2020).

We recommend that coastal managers continue to monitor rocky reef systems, as well as take advantage of long-term datasets, such as the information collected for this study (see also, Calder and Dunmore 2024). It is also important that managers incorporate environmental data, such as SST, when investigating change in seaweed communities because these communities are intrinsically linked to environmental fluctuations. However, we acknowledge that changes in SST are mainly related to varying climatic conditions and thus difficult to manage at local, regional or even national scales. We recommend that the next steps for these data should include running correlation tests to investigate

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[9] https://www.paua.org.nz/about-p%C4%81ua

changes in seaweed communities and abundances against different levels of coastal sedimentation. For example, researchers could train models to distinguish change in seawater colour and relate the colours to known quantities of fine sediment based on ground-truthing satellite imagery (e.g. satellite imagery from CawthronEye web application[10]). These models could then be tested against robust and long-term seaweed community data to provide information on change and species, or region-specific refugia. It may be more appropriate for managers in Aotearoa New Zealand to address coastal sedimentation through, for example, regeneration of native forest or estuarine plants near coasts, and to carry out this work, it is essential to have a baseline to compare change in seaweed abundance. We also recommend that researchers continue to investigate seaweed resilience to environmental variables using controlled laboratory-based experiments (e.g. Nelson 2005; Alestra and Schiel 2015; Blain and Shears 2020; Le et al. 2022; Crossett et al. 2023). These studies not only help managers forecast impacts of environmental change but also inform best practice for restoration of seaweed communities (Eger et al. 2022).

Lastly, region- and species-specific management techniques must be considered and will influence best practices for conservation and management. For example, management methods developed for the California coast in the United States may not be the most effective in locations such as Foveaux Strait in Aotearoa New Zealand. Local knowledge is also paramount, specifically for understanding when it is appropriate to undertake active restoration measures.

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[10] https://cawthroneye.cawthron.org.nz/

5. Acknowledgements

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6. References

Alestra T, Schiel DR. 2015. Impacts of local and global stressors in intertidal habitats: influence of altered nutrient, sediment and temperature levels on the early life history of three habitat-forming macroalgae. Journal of Experimental Marine Biology and Ecology. 468:29–36.

Airoldi L. 2003. The effects of sedimentation on rocky coast assemblages. Oceanography and Marine Biology Annual Review. 41:161–236.

Blain CO, Shears, NT. 2020. Differential response of forest-forming seaweeds to elevated turbidity may facilitate ecosystem shifts on temperate reefs. Marine Ecology Progress Series. 641:63–77.

Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.0-6.

Butler CL, Lucieer VL, Wotherspoon SJ, Johnson CR. 2020. Multi-decadal decline in cover of giant kelp *Macrocystis pyrifera* at the southern limit of its Australian range. Marine Ecology Progress Series. 653:1–18.

Calder S, Dunmore R. 2024. Rocky reef data layer: scoping report for potential layer update. Prepared by SLR Consulting New Zealand for Ministry for the Environment.

Castorani MCN, Harrer SL, Miller RJ, Reed DC. 2021. Disturbance structures canopy and understory productivity along an environmental gradient. Ecology Letters. 24:2192–2206.

Cavanaugh KC, Bell T, Costa M, Eddy NE, Gendall L, Gleason MG, Hessing-Lewis M, Martone R, McPherson M, Pontier O, et al. 2021. A review of the opportunities and challenges for using remote sensing for management of surface-canopy forming kelps. Frontiers in Marine Science. 8.

Connell SD. 2005. Assembly and maintenance of subtidal habitat heterogeneity: synergistic effects of light penetration and sedimentation. Marine Ecology Progress Series. 289:53–61.

Cornwall CE, Nelson WA, Aguirre JD, Blain CO, Coyle L, D’Archino R, Desmond MJ, Hepburn CD, Liggins L, Shears NT, Thomsen MS. 2023. Predicting the impacts of climate change on Aotearoa New Zealand’s seaweed-based ecosystems. Aotearoa New Zealand Journal of Botany. 63(1):1–27.

Crossett D, Dunmore R, Schiel D. 2023. Reef recovery and resilience: interpreting abiotic effects on critical early life stages of large brown algae. Marine Ecology Progress Series, 710:27–42.

Crossett D, Schattschneider J, Jamieson S. 2024. Physical and biological monitoring of Doubtful Sound / Patea: 2023–24. Nelson: Cawthron Institute. Cawthron Report 4064. Prepared for Meridian Energy Limited. [Commercial client report]

Duffy C. 1992. Shallow rocky reef habitats in Hawke’s Bay: site descriptions and rotenone collections. Wellington: Department of Conservation. Prepared for Marine Reserves Workshop: towards achieving a marine reserve network using a scientific base.

Edwards MS, Estes JA. 2006. Catastrophe, recovery and range limitation in NE Pacific kelp forests: a large-scale perspective. Marine Ecology Progress Series. 320:79–87.

Eger AM, Marzinelli EM, Christie H, Fagerli CW, Fujita D, Gonzalez AP, Hong SW, Kim JH, Lee LC, McHugh TA, et al. 2022. Global kelp forest restoration: past lessons, present status, and future directions. Biological Reviews. 97(4):1449–1475.

Erlandson JM, Graham MH, Bourque BJ, Corbett D, Estes JA, Steneck RS. 2007. The kelp highway hypothesis: marine ecology, the coastal migration theory, and the peopling of the Americas. Journal of Island and Coastal Archaeology. 2(2):161–174.

Filbee-Dexter K, Wernberg T, Grace SP, Thormar J, Fredriksen S, Narvaez CN, Feehan CJ, Norderhaug KM. 2020. Marine heatwaves and the collapse of marginal North Atlantic kelp forests. Scientific Reports. 10(1):13388.

Fox D. 2010. Rahui and marine construction: potential for enhancement of taonga species [MSc thesis]. Hamilton: University of Waikato.

Gerard VA. 1982. Growth and utilization of internal nitrogen reserves by the giant kelp *Macrocystis pyrifera* in a low-nitrogen environment. Marine Biology. 66(1):27–35.

Hollarsmith JA, Buschmann AH, Camus C, Grosholz ED. 2020. Varying reproductive success under ocean warming and acidification across giant kelp (*Macrocystis pyrifera*) populations. Journal of Experimental Marine Biology and Ecology. 522:151247.

[IPCC] Intergovernmental Panel on Climate Change. 2022. Climate Change 2022: impacts, adaptation, and vulnerability. Contribution of Working Group II to the sixth assessment report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.

Kawharu IH. 1989. Translation of the Māori text. In: Waitangi: Maori and Pakeha perspectives of the Treaty of Waitangi. Auckland: Oxford University Press.

Krumhansl KA, Okamoto DK, Rassweiler A, Novak M, Bolton JJ, Cavanaugh KC, Connell SD, Johnson CR, Konar B, Ling SD, et al. 2016. Global patterns of kelp forest change over the past half-century. Proceedings of the National Academy of Sciences of the United States of America. 113:13785–13790.

Laffoley D, Grimsditch GD, editors. 2009. The management of natural coastal carbon sinks. Gland: IUCN.

Le DM, Desmond MJ, Pritchard DW, Hepburn CD. 2022. Effect of temperature on sporulation and spore development of giant kelp (*Macrocystis pyrifera*). PLoS ONE. 17(12):e0278268.

Lindsey R, Dahlman L. 26 June 2025. Climate change: ocean heat content. [accessed 1 June 2025]. National Oceanic and Atmospheric Administration. https://www.climate.gov/news-features/understanding-climate/climate-change-ocean-heat-content

Ling SD, Scheibling RE, Rassweiler A, Johnson CR, Shears N, Connell SD, Salomon AK, Norderhaug KM, Pérez-Matus A, Hernández JC, et al. 2015. Global regime shift dynamics of catastrophic sea urchin overgrazing. Philosophical Transactions of the Royal Society B: Biological Sciences. 370:20130269.

Love T. 2018. Incorporating Māori approaches to ecosystem management in marine management – Māori Law Review. 2018:July.

Mackill R, Rennie H. 2011. The Marine and Coastal Area Act 2011. Resource Management Journal. 2011:1–7.

McCarthy A, Hepburn C, Scott N, Schweikert K, Turner R, Moller H. 2014. Local people see and care most? Severe depletion of inshore fisheries and its consequences for Māori communities in Aotearoa New Zealand. Aquatic Conservation: Marine and Freshwater Ecosystems, 24(3):369–390.

Miller KI, Balemi CA, Bell DR, Blain CO, Caiger PE, Hanns BJ, Kulins SE, Peleg O, Spyksma AJP, Shears NT. 2024. Large-scale one-off sea urchin removal promotes rapid kelp recovery in urchin barrens. Restoration Ecology. 32(1):e14060.

Miller KI, Shears NT. 2023. The efficiency and effectiveness of different sea urchin removal methods for kelp forest restoration. Restoration Ecology. 31(1):e13754.

Nelson WA. 2005. Life history and growth in culture of the endemic Aotearoa New Zealand kelp *Lessonia variegata* J. Agardh in response to differing regimes of temperature, photoperiod and light. Journal of Applied Phycology, 17(1):23–28.

Nelson WA. 2020. New Zealand seaweeds: an illustrated guide. Wellington: Te Papa Press.

Oliver ECJ, Benthuysen JA, Darmaraki S, Donat MG, Hobday AJ, Holbrook NJ, Schlegel RW, Gupta AS. 2021. Marine heatwaves. Annual Review of Marine Science. 13:313–342.

Oliver ECJ, Donat MG, Burrows MT, Moore PJ, Smale DA, Alexander LV, Benthuysen JA, Feng M, Sen Gupta A, Hobday AJ, et al. 2018. Longer and more frequent marine heatwaves over the past century. Nature Communications. 9(1):1324.

Reed DC, Foster MS. 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. Ecology (Durham). 65:937–948.

Rogers-Bennett L, Catton CA. 2019. Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. Scientific Reports. 9:1–9.

Schiel DR, Foster MS. 2006. The population biology of large brown seaweeds: ecological consequences of multiphase life histories in dynamic coastal environments. Annual Review of Ecology, Evolution, and Systematics. 37:343–372.

Schiel DR, Gerrity S, Orchard S, Alestra T, Dunmore RA, Falconer T, Thomsen MS, Tait LW. 2021. Cataclysmic disturbances to an intertidal ecosystem: loss of ecological infrastructure slows recovery of biogenic habitats and diversity. Frontiers in Ecology and Evolution. 9:767548.

Shears NT, Babcock RC. 2007. Quantitative description of mainland New Zealand's shallow subtidal reef communities. Wellington: Department of Conservation. Science for Conservation 280.

Smith JG, Free CM, Lopazanski C, Brun J, Anderson CR, Carr MH, Claudet J, Dugan JE, Eurich JG, Francis TB, et al. 2023. A marine protected area network does not confer community structure resilience to a marine heatwave across coastal ecosystems. Global Change Biology. 29(19):5634-5651.

Sneddon R, Dunmore R. 2021 Port Lyttelton Channel Deepening Project: Stage 1 benthic ecological monitoring, second post-dredging survey. Nelson: Cawthron Institute. Cawthron Report No. 3664. Prepared for Lyttelton Port Co. Ltd. [Commercial client report]

Sneddon R, Crossett D. 2024. Ecological transect surveys of Pania Reef: October 2023. Nelson: Cawthron Institute. Cawthron Report 4028. Prepared for Port of Napier Ltd. [Commercial client report]

Straub SC, Wernberg T, Thomsen MS, Moore PJ, Burrows MT, Harvey BP, Smale DA. 2019. Resistance, extinction, and everything in between – the diverse responses of seaweeds to marine heatwaves. Frontiers in Marine Science. 6:763.

Stokes E. 1992. The treaty of Waitangi and the Waitangi tribunal: Maori claims in New Zealand. Applied Geography. 12:2:176-191.

Taikato VR. 2021. Ahumoana tawhito (ancient aquaculture): the translocation of toheroa (*Paphies ventricosa*) and other marine species by Māori [PhD thesis]. Hamilton: University of Waikato.

Tait LW. 2019. Giant kelp forests at critical light thresholds show compromised ecological resilience to environmental and biological drivers. Estuarine, Coastal and Shelf Science. 219:231–241.

Tait LW, Thoral F, Pinkerton MH, Thomsen MS, Schiel DR. 2021. Loss of giant kelp, *Macrocystis pyrifera*, driven by marine heatwaves and exacerbated by poor water clarity in Aotearoa New Zealand. Frontiers in Marine Science. 8.

Thomsen MS, Mondardini L, Alestra T, Gerrity S, Tait L, South PM, Lilley SA, Schiel DR. 2019. Local extinction of bull kelp (*Durvillaea* spp.) due to a marine heatwave. Frontiers in Marine Science. 6.

Thoral F, Montie S, Thomsen MS, Tait LW, Pinkerton MH, Schiel DR. 2022. Unravelling seasonal trends in coastal marine heatwave metrics across global biogeographical realms. Scientific Reports. 12:7740.

Urlich SC, Handley SJ. 2020. From 'clean and green' to 'brown and down': a synthesis of historical changes to biodiversity and marine ecosystems in the Marlborough Sounds, New Zealand. Ocean & Coastal Management. 198:105349.

Wassilieff M. 2009. Seaweed – traditional use of seaweeds. In: Te Ara – the Encyclopedia of New Zealand. [accessed 24 June 2025]. https://teara.govt.nz/en/seaweed/page-4

Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen MF. 2019. Chapter 3 – Status and trends for the world's kelp forests. In: Sheppard C, editor. World seas: an environmental evaluation. 2nd edition. London: Academic Press. p. 57–78.

White LN, White WL. 2020. Seaweed utilisation in New Zealand. Botanica Marina. 63(4):303–313.

Wickham H. 2016. ggplot2: elegant graphics for data analysis. New York: Springer-Verlag. https://ggplot2.tidyverse.org

Wing SR, Shears NT, Tait LW, Schiel DR. 2022. The legacies of land clearance and trophic downgrading accumulate to affect structure and function of kelp forests. Ecosphere 13:12:e4303.

Zimmerman R, Kremer J. 1984. Episodic nutrient supply to a kelp forest ecosystem in Southern California. Journal of Marine Research. 42(3):591–604.

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