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# Co-occurring foundation species increase habitat heterogeneity across estuarine intertidal environments on the South Island of New Zealand

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ABSTRACT

Estuaries are traditionally considered sedimentary 'bare' ecosystems, dominated by infauna that bury into sediments to avoid being eaten by fish or birds. However, estuaries can be converted to biogenic complex 'hard' habitats, like seagrass beds, seaweed patches or surface-deposits of live or dead shells. Furthermore, habitat heterogeneity is enhanced if these foundation species co-occur. Still, few studies have quantified abundances and co-occurrences of different types of foundation species along spatiotemporal stress gradients. We therefore quantified abundances of seagrasses (*Zostera muelleri*), seaweeds (*Ulva* spp., *Gracilaria chilensis*), surface deposited dead shells and densities of dominant and partly buried cockles (*Austrovenus stutchburyi*) in estuaries on the South Island of New Zealand. A total of 927 large-scale drone images, 1264 small-scale camera images, and 160 sediment-quadrats were collected from 32 common estuarine environments (fully crossed 5-factorial surveys with 2 latitudes x 2 sites x 2 intertidal elevations x 2 seasons x 2 intra-seasonal sampling months). Across the 32 environments, seagrass was most abundant (19–22 % cover, depending on sampling method), followed by shells (9–13 %) and seaweed (4 %). Scattered seaweed and shells were, despite their low cover, ubiquitous in the 32 environments, and seagrasses always co-occurred with shells and/or seaweed. The spatial gradients had a stronger influence on abundances of foundation species than temporal factors, that mainly affected seaweed and live cockles, with high (70 %), medium (50 %) and low (30 %) statistical agreement between analysis of drone vs. camera images for seaweed, shells and seagrass, respectively. Finally, correlation analysis revealed negative associations between seagrasses and both shells and seaweed, but with large variation between seasons. Our study highlights that foundation species rarely occur as single-species stands, and that the ecological impacts of scattered seaweeds and dead surface-deposited shells within seagrass beds should be studied in more detail. Our findings also underscore the critical role of spatiotemporal stressors in shaping estuarine ecosystems and highlight the importance of using supplementary sampling methods to inform management strategies for estuaries in the face of environmental change.

## 1. Introduction

Foundation species (hereafter FS), like trees, salt marshes and corals, are large conspicuous and abundant organisms that modify abiotic conditions and ecosystem functions, increase habitat heterogeneity by building physical structures, and typically increase biodiversity (Dayton, 1972; Ellison et al., 2005; Ellison, 2019; Lamy et al., 2020; Thomsen et al., 2022). Many studies have documented the distribution and abundance of a particular type of FS (e.g., see papers above), although recent studies have highlighted that multiple FS with different form and functions sometimes co-occur and thereby increase habitat heterogeneity, e.g., between trees and epiphytes, mussels and salt marsh plants, or seaweed and sessile habitat-forming invertebrates (Yakovis et al., 2008; Thomsen et al. 2010, 2018; Angelini et al., 2011; Thyrring et al., 2015). FS are particularly important in shallow sedimentary estuarine ecosystems, where they increase habitat heterogeneity by converting 'bare' mud to systems dominated by different forms of biogenic structures, including (a) slower-growing clonal and persistent seagrasses, (b) faster-growing solitary but more ephemeral seaweeds, or (c) shell-forming species, like filter or deposit feeding bivalves, that

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leave biological legacies (shells) when they die (Gutiérrez et al., 2003; Saldaña et al., 2024). The vast majority of research have studied seagrass, seaweed or shell-formers as functional monocultures dominated by a single type of FS, although these different FS sometimes co-occur and thereby increase habitat heterogeneity (Thomsen et al., 2013; Clemente and Thomsen, 2023).

Seagrasses typically form dense meadows that increase habitat heterogeneity and biodiversity, serve as nurseries for juvenile fish, and stabilize sediments (Orth et al., 2006; McGlathery et al., 2007; Fortes, 2012; Honda et al., 2013). Seagrasses also improve water quality through their nutrient cycling, enhance ecosystem resilience, and sequester carbon from the atmosphere and potentially contribute to climate change mitigation (Duffy, 2006; Marbà et al., 2015; Trevathan-Tackett et al., 2017; Mazarrasa et al., 2021, Reyes et al., 2022). However, quantifying distributions of seagrasses remains challenging, especially in estuaries where they often are smaller and sparser and typically form inconspicuous patches (Thomsen et al., 2016a; Pullen et al., 2022). Although remote sensing has been useful for automated monitoring of seagrass beds over large spatiotemporal scales (Hossain et al., 2015; Veettil et al., 2020) the resolution of satellite images generally fail to capture finer details of the seascape, or smaller and sparser patches build by small seagrass species (Dekker et al., 2005). Estuarine seaweeds also increase habitat heterogeneity and provide resources for associated fauna (Gartner et al., 2013; Dijkstra et al., 2017; Ramus et al., 2017; Cotas et al., 2023). However, their smaller sizes, fluctuating populations, scattered distributions, and, for green seaweeds, similar reflectance properties to seagrasses, complicate identification from remote sensing images (Clemente et al., 2023). Finally, shell-forming mollusks, like infaunal bivalves, often dominate in estuaries – including in and around estuarine seagrass beds (Gutiérrez et al., 2003; Thyrring et al., 2015; Lohrer et al., 2016; Tomatsuri and Kon, 2017; Clemente and Thomsen, 2024). Bivalves also affect sediment stability and nutrient cycling through bioturbation and filter-feeding activities (Lelieveld et al., 2004; Donadi et al., 2014; Lohrer et al., 2016). Furthermore, bivalves increase habitat heterogeneity when their dead shells accumulate on the sediment surface, altering microhabitat conditions and providing hard substratum for species like many seaweeds, limpets and sea anemones (Summerhayes et al., 2009; Tomatsuri and Kon, 2017; Saldaña et al., 2024). However, the ecological roles of surface-deposited dead shells remain understudied and, like their living counterpart, are near-impossible to detect with satellite images due to their very small sizes, irregular distribution and low reflectance.

Here we address research gaps outlined above, as we measured abundances and co-occurrences of seagrass, seaweed, and shells, and how their distributions varied between sampling scales and estuarine environments, to cover typical stress gradient that covary with temperature (latitudes, seasons, within-seasonal sampling months), salinity (site effects) and desiccation stress (elevation levels). Specifically, we quantified abundances and co-occurrences of the small seagrass *Zostera muelleri* Irmisch ex Asch., the seaweeds *Ulva* spp. (hereafter *Ulva*), and *Gracilaria chilensis* C. J. Bird, McLachlan & E. C. Oliveira 1986 (hereafter *Gracilaria*), and the ubiquitous endemic bivalve *Austrovenus stutchburyi* (Wood, 1828) – particularly its surface deposited dead shells - in estuaries on the South Island of New Zealand. Furthermore, we tested if their abundances varied across sampling scales and spatiotemporal stress gradients, including latitudes, sites, elevations, seasons, and intra-seasonal sampling months. We combined and compared drone and handheld camera surveys to provide high resolution alternative to satellite images and better detect smaller and scattered FS. Here, drone images offer a high-resolution aerial perspective that cover large areas (Martin et al., 2020; Chand and Bollard, 2022) whereas handheld camera images allow for finer-scale observations (e.g., of individual shells and small seaweed fragments) that complement and validate drone imagery (Hamad et al., 2022; Clemente and Thomsen, 2024).

## 2. Methods

### 2.1. Field sampling

We sampled estuarine seagrasses, seaweeds, and shells on the South Island of New Zealand in fully crossed five-factorial surveys to represent 32 typical estuarine environments, covering two latitudes (warmer northern vs. colder southern), two sites with different proximities to estuary mouths (near: typically 1 km vs. far: up to 5 km from the mouth), two vertical elevations (low vs. mid intertidal zones, with a vertical difference of *ca.* 30–50 cm), two seasons (summer vs. winter) and two periods within each season (a warmer vs. colder month based on long-term average monthly temperatures, Table S2 - see also Fig. 1 for map of study sites and Tables S1–S3 for descriptions of all the test factors, survey locations, sampling dates and typical temperature conditions). To quantify FS over larger areas, a drone was deployed during low tide to cover the above-mentioned 32 estuarine environments. We used a DJI Mavic Pro (FC220) equipped with a 12.35 MP 1/2.3" sensor (CMOS, 4000 x 3000 pixels), to capture nadir-viewing still images at 10 m altitude, where each images covered ca. ~100 $m^2$. Each drone flight followed a pre-programmed path set in *Pix4D Capture* app to constrain the flight within a designated Area Of Interest (AOI) corresponding to ~10,000 $m^2$ of the intertidal zone. This approach ensured consistency of spatial extent across all sampling events. Approximately 200 drone images were collected for each of the 32 environments (i.e., all combinations of *latitude* × *site* × *elevation* × *season* × *intra-season*). The geotagged drone images were map-viewed and sorted according to elevation levels and randomly selected from the whole drone image library (ensuring that no images are overlapping and maximizing statistical independence). For each image, the percent cover of seagrass (*Z. muelleri)*, seaweeds (dominated by *Ulva*, but also including a few scattered *Gracilaria* patches), and surface-deposited shells (almost entirely from *A. stutchburyi*) were visually quantified using a superimposed 100-cell grid. Quality controls included flagging images that were blurred or covered in water and these images were later excluded prior to statistical analyses. To supplement and validate the broad-scale drone imagery, fine-scale patch-level surveys were performed at the same sites and dates as the drone surveys. Nadir-viewing still images were taken using a Nikon Coolpix AW130 camera positioned ca. 1 m above the surface. Approximately 50 camera images were collected for each of the 32 environments. Geotagged images covered ca. 1 $m^2$ and were taken more than 2 m apart within the same area as the drone surveys. Camera images were analyzed as described for the drone survey, with similar quality controls. It is important to note that nadir images can only show coverage of a single top canopy layer, not any smaller subcanopy species, including infaunal cockles buried in sediments. We therefore supplemented the image surveys with a hands-on survey collecting live cockles in 0.0625 $m^2$ quadrats in the same 32 environments with five replicates sampled ca. 5 m apart, resulting in a total of 160 sampled quadrats. Within each quadrat, all live cockles were collected, rinsed, placed onto a white tray with a ruler for scale, photographed, and then returned to their original sediment location. Densities and shell-length were quantified from each image using *ImageJ* software.

### 2.2. Data analysis

First, co-occurrence patterns were explored graphically by transforming percent cover to presence-absence and re-classifying each image to show mud-only or being inhabited by a single FS (shells, seagrass, seaweed), two FS (three possible combinations) or all three FS. Second, we analyzed cover and density data with fixed five-factorial permutation ANOVAs (perANOVA, with 999 permutations). All test factors were considered fixed, because treatments for each test factors can be interpreted to represent contrasting environmental conditions, like high vs low desiccation (elevation), sites with low vs high salinity

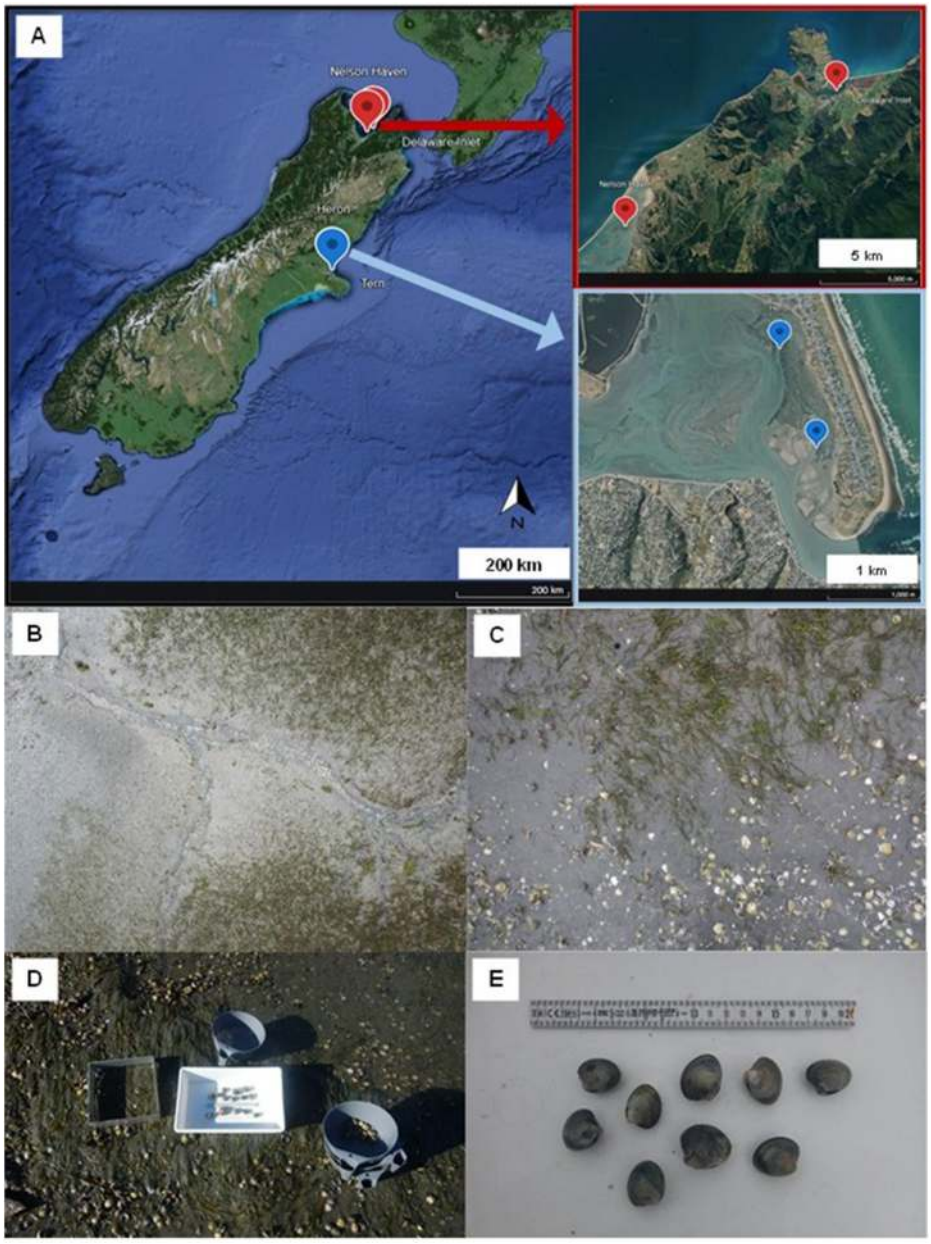


**Fig. 1.** A) Locations of study sites in the northern (red inset) and southern (blue inset) areas of the South Island, New Zealand. B) Example of a typical drone image at 10 m altitude, showing seagrass distribution. C) Example of a typical hand camera image at 1 m altitude, capturing close-up details of seagrass, seaweed and surface deposited shells. D) Quadrat sampling setup for measuring live cockles (*Austrovenus*) in the field. E) Sampled live cockle shells scaled with ruler. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(proximity to open ocean), or warmer vs colder conditions (latitude, season, intraseason). Recurring sampling within a season is sometimes considered a nested random factor, but here we consider it fixed, to test for small scale temperature differences, analog to other recurrent intra-seasonal tests, like contrasting day vs night sampling (Adrian and Meeuwig, 2001; Ribeiro et al., 2006; Azzurro et al., 2007; Connan et al., 2007; Thomsen et al., 2016b; Barton and Schmitz, 2018), before vs after disturbances (Teixido et al., 2013; Zink et al., 2020; Zhang et al., 2022) or (like us) warmer vs colder intra-seasonal periods (Okoola, 2000; McKinnon et al., 2008, González et al., 2015, Magnani et al., 2017; Montie and Thomsen, 2023b, 2023a, Clemente and Thomsen, 2025). Prior to analyses, images with extremely low cover (combined cover of all FS $\leq$ 1 %) were excluded to minimize statistical bias. Cover and density data were arcsine square root and square root transformed, respectively, to reduce variance heterogeneity. PerANOVA is robust to non-normality and unbalanced replicates, but variances were heterogeneous also after transformations (Levene's Test, $p < 0.05$) and alpha was therefore adjusted to 0.01 (Underwood, 1997). Finally, we tested if the percent cover of FS had positive or negative (or no) associations, using Spearman rank correlations (data did not meet linearity assumptions). Correlations were done pairwise for seaweed vs. seagrass, shell vs. seagrass, and shell vs. seaweed, for drone and camera images separately and for each season (summer vs. winter) – the latter to examine if temperature conditions can switch interaction signs, from facilitation to competition, or vice versa. Additional analyses with different space-time combinations (latitude, elevation, season) are described in the supplement.

## 3. Results

### 3.1. Overview

Analysis of the 927 drone images and 1264 camera images showed that seagrasses were the most abundant foundation species (FS, 19 and 22 % cover in drone and camera images, respectively) followed by surface-deposited shells (9 % drone, 13 % camera) and seaweed (4 % for both methods). Graphical analysis of cover data reclassified to presence-absence (Fig. 2), demonstrated that FS were observed in every single image. We also found that surface deposited shells were ubiquitous across the 32 environments, observed in 99.5 % of the images (minus 12 images where seaweed and seagrass co-occurred). Seagrasses were also common across the 32 environments (in 74 % of all images) and seagrass was never observed as single FS. Similarly, seaweed was, like seagrass, never observed alone, and, despite their very low cover (see above), were present in more images (81 %) than seagrass. Furthermore, detection of co-occurrences increased with increasing scale, e.g., the three FS co-occurred in 69 % of drone images compared to 51 % of camera images. We also found that the abundances of FS were consistently affected by spatial test-factors (latitude, site, elevation) whereas temporal test-factors (season, intra-season) impacted seaweed and live shell densities, but with less impact on seagrasses, dead shells, and the length of cockle shells. Comparison of the significant results from the perANOVAs (Tables 1 and 2) generally showed good agreement between drone and photo data for seaweed abundances (70 % of the significant results were similar), moderate agreement for shells (50 %) and weak agreement for seagrasses (30 %). The cover of shells and seagrasses, and seaweed and seagrasses, were negatively correlated with strong agreement between drone and camera images. However, the cover of shells and seaweed was not correlated for the camera images and switched from a positive correlation in summer to negative in winter for the drone


**Fig. 2. Co-occurrences between foundation species across estuarine environments from drone and camera images.** Percentage of images inhabited by different combinations of surface deposited shells (Sh), seaweed (Sw), and seagrass (Sg) across different latitudes (North-South), distances to the ocean (Far-Near), elevations (Mid-Low), seasons (Summer-Winter) and intraseasonal sampling months (Warmer-Colder, adjacent bars, in that order). See supplement for replication levels.

**Table 1**
**ANOVA for foundation species in Drone images.** Fixed permutational analysis of variance (perANOVA) of arcsine square-root-transformed percent cover data for seagrass, seaweeds, and surface-deposited shells obtained from drone images. Significant *p-values* are boldfaced for alpha ≤0.01 (heterogeneous variances, see Methods). Significant results with %SS ≥ 10 % and 1 % ≤ %SS < 10 % are highlighted in red and blue, respectively. Shading is based on actual %SS values prior to rounding ($N_{total}$ = 927, Df = 1 for all test factors; Df residuals = 895).

| | SEAGRASS | | | | SEAWEED | | | | SHELL | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Source of variation** | **SS** | **%SS** | **F** | **P** | **SS** | **%SS** | **F** | **P** | **SS** | **%SS** | **F** | **P** |
| Latitude (Lat) | 4.97 | 6.0 | 130.8 | **0.000** | 1.259 | 12.1 | 442.0 | **0.000** | 0.22 | 1.0 | 16.8 | **0.000** |
| Site (Sit) | 3.62 | 4.4 | 95.2 | **0.000** | 0.281 | 2.7 | 98.8 | **0.000** | 4.22 | 18.9 | 325.8 | **0.000** |
| Elevation (Ele) | 25.27 | 30.5 | 665.6 | **0.000** | 0.175 | 1.7 | 61.3 | **0.000** | 0.79 | 3.5 | 60.9 | **0.000** |
| Season (Sea) | 0.40 | 0.5 | 10.6 | **0.001** | 1.639 | 15.7 | 575.7 | **0.000** | 0.19 | 0.8 | 14.6 | **0.000** |
| Intraseason (IntraSea) | 0.27 | 0.3 | 7.0 | **0.008** | 0.240 | 2.3 | 84.2 | **0.000** | 0.00 | 0.0 | 0.0 | 0.972 |
| Lat x Sit | 0.23 | 0.3 | 6.0 | 0.014 | 0.816 | 7.8 | 286.7 | **0.000** | 1.02 | 4.6 | 78.5 | **0.000** |
| Lat x Ele | 11.50 | 13.9 | 302.9 | **0.000** | 0.070 | 0.7 | 24.6 | **0.000** | 2.35 | 10.5 | 181.3 | **0.000** |
| Sit x Ele | 0.68 | 0.8 | 17.8 | **0.000** | 0.026 | 0.3 | 9.3 | **0.002** | 0.11 | 0.5 | 8.7 | **0.003** |
| Lat x Sea | 0.36 | 0.4 | 9.4 | **0.002** | 1.286 | 12.3 | 451.5 | **0.000** | 0.09 | 0.4 | 6.8 | **0.009** |
| Sit x Sea | 0.19 | 0.2 | 4.9 | 0.027 | 0.103 | 0.98 | 36.2 | **0.000** | 0.02 | 0.1 | 1.2 | 0.274 |
| Ele x Sea | 0.08 | 0.1 | 2.2 | 0.138 | 0.054 | 0.5 | 18.8 | **0.000** | 0.01 | 0.1 | 1.0 | 0.328 |
| Lat x IntraSea | 0.00 | 0.0 | 0.0 | 0.953 | 0.099 | 0.9 | 34.6 | **0.000** | 0.01 | 0.0 | 0.4 | 0.513 |
| Sit x IntraSea | 0.01 | 0.0 | 0.2 | 0.691 | 0.018 | 0.2 | 6.2 | 0.013 | 0.10 | 0.5 | 8.0 | **0.005** |
| Ele x IntraSea | 0.00 | 0.0 | 0.0 | 0.923 | 0.003 | 0.0 | 1.2 | 0.281 | 0.01 | 0.1 | 1.1 | 0.285 |
| Sea x IntraSea | 0.05 | 0.1 | 1.2 | 0.274 | 0.178 | 1.7 | 62.5 | **0.000** | 0.05 | 0.2 | 3.8 | 0.050 |
| Lat x Sit x Ele | 0.24 | 0.3 | 6.4 | 0.011 | 0.042 | 0.4 | 14.6 | **0.000** | 0.87 | 3.9 | 67.3 | **0.000** |
| Lat x Sit x Sea | 0.05 | 0.1 | 1.3 | 0.251 | 0.762 | 7.3 | 267.7 | **0.000** | 0.00 | 0.0 | 0.0 | 0.909 |
| Lat x Ele x Sea | 0.13 | 0.2 | 3.4 | 0.066 | 0.007 | 0.1 | 2.5 | 0.113 | 0.02 | 0.1 | 1.9 | 0.169 |
| Sit x Ele x Sea | 0.12 | 0.1 | 3.1 | 0.079 | 0.005 | 0.0 | 1.6 | 0.204 | 0.06 | 0.3 | 5.0 | 0.026 |
| Lat x Sit x IntraSea | 0.25 | 0.3 | 6.5 | 0.011 | 0.015 | 0.1 | 5.1 | 0.024 | 0.00 | 0.0 | 0.1 | 0.732 |
| Lat x Ele x IntraSea | 0.02 | 0.0 | 0.6 | 0.437 | 0.027 | 0.3 | 9.6 | **0.002** | 0.01 | 0.1 | 1.1 | 0.296 |
| Sit x Ele x IntraSea | 0.01 | 0.0 | 0.3 | 0.594 | 0.012 | 0.1 | 4.1 | 0.042 | 0.05 | 0.2 | 3.7 | 0.055 |
| Lat x Sea x IntraSea | 0.06 | 0.1 | 1.7 | 0.198 | 0.521 | 5.0 | 183.1 | **0.000** | 0.03 | 0.1 | 2.6 | 0.109 |
| Sit x Sea x IntraSea | 0.07 | 0.1 | 1.8 | 0.181 | 0.050 | 0.5 | 17.5 | **0.000** | 0.06 | 0.3 | 4.9 | 0.027 |
| Ele x Sea x IntraSea | 0.03 | 0.0 | 0.7 | 0.391 | 0.000 | 0.0 | 0.1 | 0.823 | 0.01 | 0.0 | 0.7 | 0.389 |
| Lat x Sit x Ele x Sea | 0.09 | 0.1 | 2.5 | 0.116 | 0.000 | 0.0 | 0.0 | 0.866 | 0.05 | 0.2 | 3.5 | 0.062 |
| Lat x Sit x Ele x IntraSea | 0.04 | 0.1 | 1.1 | 0.290 | 0.039 | 0.4 | 13.8 | **0.000** | 0.24 | 1.1 | 18.2 | **0.000** |
| Lat x Sit x Sea x IntraSea | 0.00 | 0.0 | 0.0 | 0.972 | 0.090 | 0.9 | 31.5 | **0.000** | 0.12 | 0.5 | 9.1 | **0.003** |
| Lat x Ele x Sea x IntraSea | 0.12 | 0.1 | 3.0 | 0.081 | 0.005 | 0.0 | 1.6 | 0.205 | 0.00 | 0.0 | 0.1 | 0.768 |
| Sit x Ele x Sea x IntraSea | 0.11 | 0.1 | 2.8 | 0.095 | 0.000 | 0.0 | 0.1 | 0.766 | 0.00 | 0.0 | 0.0 | 0.912 |
| Lat x Sit x Ele x Sea x IntraSea | 0.02 | 0.0 | 0.4 | 0.506 | 0.061 | 0.6 | 21.3 | **0.000** | 0.03 | 0.1 | 2.1 | 0.144 |
| Residuals | 33.99 | 41.0 | | | 2.549 | 24.4 | | | 11.59 | 51.9 | | |

images. Below, we detail these results, focusing on significant results that explained >1 % of total sum of squares (SS) in ANOVA tests to simplify data interpretations, i.e., we assume that statistically significant results explaining minimal variance have limited ecological importance.

### 3.2. Abundances and sizes

*Seagrass.* The ANOVA models for seagrass explained 59.0 % of the SS for drone images but only 38.5 % for camera images. Seagrass cover was significantly affected by six interactions that explained >1 % of SS (Tables 1 and 2). There were no significant 3-way interactions for the drone images, but three for the camera images; *Latitude* x *Site* x *Elevation*

**Table 2**
**ANOVA for foundation species in camera images.** Fixed permutational analysis of variance (perANOVA) of arcsine square-root-transformed percent cover of seagrass, seaweeds, and surface deposited shells obtained from camera images. Significant *p-values* are boldfaced for alpha ≤0.01 (heterogeneous variances, see Methods). Significant results with %SS ≥ 10 % and 1 % ≤ %SS < 10 % are highlighted in red and blue, respectively. Shading is based on actual %SS values prior to rounding ($N_{total}$ = 1264, Df = 1 for all test factors, Df residuals = 1232).

| | SEAGRASS | | | | SEAWEED | | | | SHELL | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Source of variation** | **SS** | **%SS** | **F** | **P** | **SS** | **%SS** | **F** | **P** | **SS** | **%SS** | **F** | **P** |
| Latitude (Lat) | 2.95 | 2.0 | 40.6 | **0.000** | 4.409 | 19.1 | 608.6 | **0.000** | 2.82 | 3.8 | 80.7 | **0.000** |
| Site (Sit) | 7.53 | 5.2 | 103.5 | **0.000** | 0.090 | 0.4 | 12.4 | **0.000** | 12.50 | 16.7 | 357.1 | **0.000** |
| Elevation (Ele) | 15.21 | 10.4 | 209.2 | **0.000** | 0.330 | 1.4 | 45.5 | **0.000** | 2.31 | 3.1 | 65.9 | **0.000** |
| Season (Sea) | 1.58 | 1.1 | 21.7 | **0.000** | 2.593 | 11.3 | 357.9 | **0.000** | 1.20 | 1.6 | 34.2 | **0.000** |
| Intraseason (IntraSea) | 0.35 | 0.2 | 4.9 | 0.028 | 0.486 | 2.1 | 67.0 | **0.000** | 0.02 | 0.0 | 0.6 | 0.456 |
| Lat x Sit | 7.21 | 5.0 | 99.2 | **0.000** | 0.764 | 3.3 | 105.4 | **0.000** | 0.00 | 0.0 | 0.0 | 0.912 |
| Lat x Ele | 4.64 | 3.2 | 63.8 | **0.000** | 0.030 | 0.1 | 4.2 | 0.042 | 5.78 | 7.7 | 165.0 | **0.000** |
| Sit x Ele | 0.29 | 0.2 | 4.0 | 0.045 | 0.301 | 1.3 | 41.6 | **0.000** | 0.28 | 0.4 | 8.0 | **0.005** |
| Lat x Sea | 0.19 | 0.1 | 2.7 | 0.103 | 1.373 | 6.0 | 189.5 | **0.000** | 1.01 | 1.4 | 28.9 | **0.000** |
| Sit x Sea | 0.47 | 0.3 | 6.5 | 0.011 | 0.014 | 0.1 | 1.9 | 0.171 | 0.00 | 0.0 | 0.0 | 0.835 |
| Ele x Sea | 0.63 | 0.4 | 8.7 | **0.003** | 0.018 | 0.1 | 2.4 | 0.120 | 0.02 | 0.0 | 0.5 | 0.490 |
| Lat x IntraSea | 1.31 | 0.9 | 18.0 | **0.000** | 0.076 | 0.3 | 10.5 | **0.001** | 0.11 | 0.2 | 3.3 | 0.071 |
| Sit x IntraSea | 0.02 | 0.0 | 0.2 | 0.628 | 0.080 | 0.3 | 11.0 | **0.001** | 0.00 | 0.0 | 0.1 | 0.780 |
| Ele x IntraSea | 0.17 | 0.1 | 2.3 | 0.131 | 0.040 | 0.2 | 5.5 | 0.020 | 0.02 | 0.0 | 0.5 | 0.478 |
| Sea x IntraSea | 1.06 | 0.7 | 14.6 | **0.000** | 1.050 | 4.6 | 145.0 | **0.000** | 0.48 | 0.6 | 13.7 | **0.000** |
| Lat x Sit x Ele | 4.10 | 2.8 | 56.4 | **0.000** | 0.227 | 0.98 | 31.3 | **0.000** | 2.85 | 3.8 | 81.3 | **0.000** |
| Lat x Sit x Sea | 1.79 | 1.2 | 24.7 | **0.000** | 0.706 | 3.1 | 97.4 | **0.000** | 0.63 | 0.8 | 17.9 | **0.000** |
| Lat x Ele x Sea | 0.00 | 0.0 | 0.0 | 0.911 | 0.018 | 0.1 | 2.4 | 0.119 | 0.00 | 0.0 | 0.1 | 0.716 |
| Sit x Ele x Sea | 0.06 | 0.0 | 0.8 | 0.376 | 0.010 | 0.0 | 1.3 | 0.250 | 0.06 | 0.1 | 1.8 | 0.184 |
| Lat x Sit x IntraSea | 0.40 | 0.3 | 5.5 | 0.019 | 0.001 | 0.0 | 0.1 | 0.737 | 0.00 | 0.0 | 0.0 | 0.842 |
| Lat x Ele x IntraSea | 0.18 | 0.1 | 2.5 | 0.117 | 0.000 | 0.0 | 0.0 | 0.926 | 0.14 | 0.2 | 4.1 | 0.044 |
| Sit x Ele x IntraSea | 0.94 | 0.6 | 13.0 | **0.000** | 0.001 | 0.0 | 0.1 | 0.783 | 0.20 | 0.3 | 5.8 | 0.016 |
| Lat x Sea x IntraSea | 2.58 | 1.8 | 35.5 | **0.000** | 0.668 | 2.9 | 92.3 | **0.000** | 0.84 | 1.1 | 23.9 | **0.000** |
| Sit x Sea x IntraSea | 0.35 | 0.2 | 4.8 | 0.029 | 0.021 | 0.1 | 3.0 | 0.085 | 0.03 | 0.0 | 0.7 | 0.395 |
| Ele x Sea x IntraSea | 0.12 | 0.1 | 1.7 | 0.194 | 0.019 | 0.1 | 2.7 | 0.102 | 0.05 | 0.1 | 1.3 | 0.251 |
| Lat x Sit x Ele x Sea | 0.39 | 0.3 | 5.4 | 0.020 | 0.004 | 0.0 | 0.6 | 0.455 | 0.04 | 0.1 | 1.2 | 0.267 |
| Lat x Sit x Ele x IntraSea | 0.06 | 0.0 | 0.9 | 0.346 | 0.005 | 0.0 | 0.7 | 0.398 | 0.04 | 0.1 | 1.1 | 0.296 |
| Lat x Sit x Sea x IntraSea | 0.58 | 0.4 | 8.0 | **0.005** | 0.516 | 2.2 | 71.3 | **0.000** | 0.12 | 0.2 | 3.5 | 0.060 |
| Lat x Ele x Sea x IntraSea | 0.50 | 0.3 | 6.9 | **0.009** | 0.014 | 0.1 | 2.0 | 0.160 | 0.00 | 0.0 | 0.1 | 0.781 |
| Sit x Ele x Sea x IntraSea | 0.29 | 0.2 | 4.0 | 0.046 | 0.100 | 0.4 | 13.8 | **0.000** | 0.16 | 0.2 | 4.7 | 0.030 |
| Lat x Sit x Ele x Sea x IntraSea | 0.09 | 0.1 | 1.2 | 0.277 | 0.146 | 0.6 | 20.1 | **0.000** | 0.05 | 0.1 | 1.5 | 0.228 |
| Residuals | 89.59 | 61.5 | | | 8.926 | 38.8 | | | 43.13 | 57.6 | | |

(2.8 %), *Latitude* x *Season* x *Intra-season* (1.8 %) and *Latitude* x *Site* x *Season* (1.2 %). We found one significant two-way interaction for the drone images (*Latitude* x *Elevation* = 13.9 %) and two for camera images (*Latitude* x *Site* = 5.0 % and *Latitude* x *Elevation* = 3.2 %). Notably, among these interactions, seagrass was most abundant at the mid-tide level in colder latitudes (Figs. 3A and 4A). Most main effects were significant. For drone images, the most important test factor was *Elevation* (30.5 %), followed by *Latitude* (6.0 %) and *Site* (4.4 %). Results were relatively similar for camera photos where the most important factor again was *Elevation* (10.4 %), followed by *Site* (5.2 %), *Latitude* (2.0 %) and *Season* (1.1 %). Seasonal and intra-seasonal sampling had little effect on seagrass cover from the drone images, whereas cover derived from camera images was higher during summer months at the southern latitude estuaries (Fig. 3A). Both methods showed that seagrasses generally were more abundant in the southern latitude estuaries, far-ocean sites, and mid elevations (Figs. 3A and 4A).

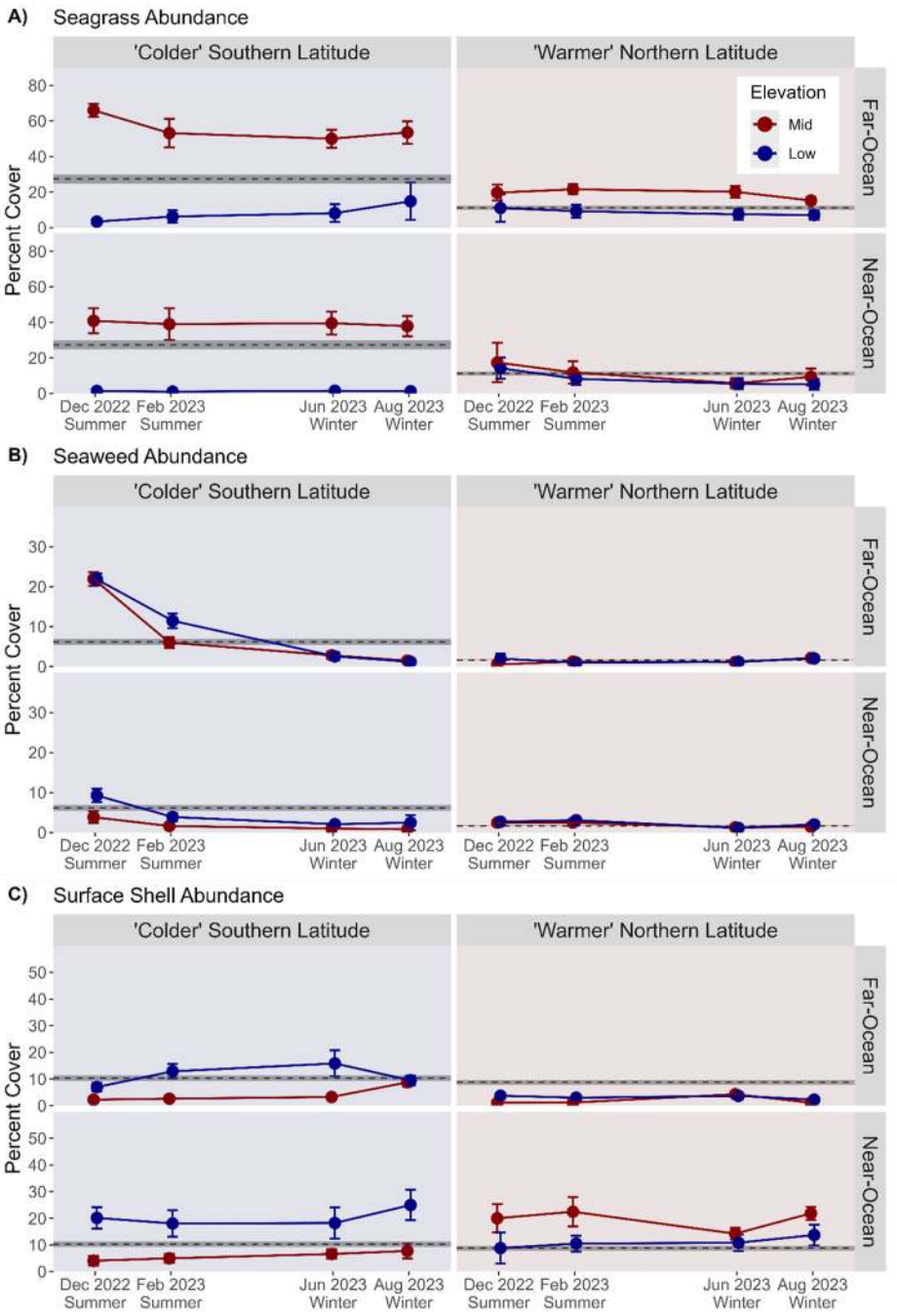


**Fig. 3. Abundance of foundation species from drone images**. Percent cover (mean ± 95 % CLs) of (A) seagrass, (B) seaweed, and (C) surface-deposited shells sampled across latitudes (northern vs. southern), sites (far vs. near ocean), elevation (mid vs. low), seasons (winter vs. summer), and intra-seasons (colder Dec 2022 & Aug 2023 vs. warmer Feb & Jun 2023). The horizonal dashed line is the overall mean ± 95 % CLs for each latitude (on average $n = 30$s).

*Seaweed.* The ANOVA model explained a high proportion of SS for seaweed (75.6 % vs 61.2 % for drone and camera images, respectively). A four-way interaction (*Latitude* x *Site* x *Season* x *Intra-season*) explained 2.2 % SS in the camera-based data. In addition, seaweed cover was significantly influenced by four three-way interactions that explained >1 % of the SS, with similar results between drone and camera images (Tables 1 and 2). More specifically, *Latitude* x *Site* x *Elevation* was most important (7.3 vs. 3.1 %), followed by *Latitude* x *Season* x *Intra-season* (5.0 vs 2.9 %). Two-way interactions were also relatively similar between the scaling methods. For drone images the most important 2-way interactions were *Latitude* x *Season* (12.3 %), followed by *Latitude* x *Site* (7.8 %) and *Season* x *Intra-season* (1.7 %). By comparison the most important significant 2-way interactions for camera images were again *Latitude* x *Season* (6.0 %), followed by *Season* x *Intra-season* (4.6 %), *Latitude* x *Site* (3.3 %) and *Site* x *Elevation* (1.3 %). These results highlight that seaweed cover generally was higher at Southern sites but particular so in summer months (Figs. 3Band 4B). Results were also relatively similar between methods for the main effects. Analyses of the drone images showed the following ranking: *Season* (15.7 %) > *Latitude* (12.1 %) > *Site* (2.7 %) > *Intra-season* (2.3 %) > *Elevation* (1.7 %), whereas test factors for the camera images were ranked as *Latitude* (19.1 %) > *Season* (11.3 %) > *Intra-season* (2.1 %) > *Elevation* (1.4 %). Seaweed cover was generally higher in the southern latitude estuaries, during summer, and to a lesser extent at far-ocean sites and lower elevations (Figs. 3B and 4B).

*Surface shells.* Only 48.1 % and 42.4 % of the SS were explained for

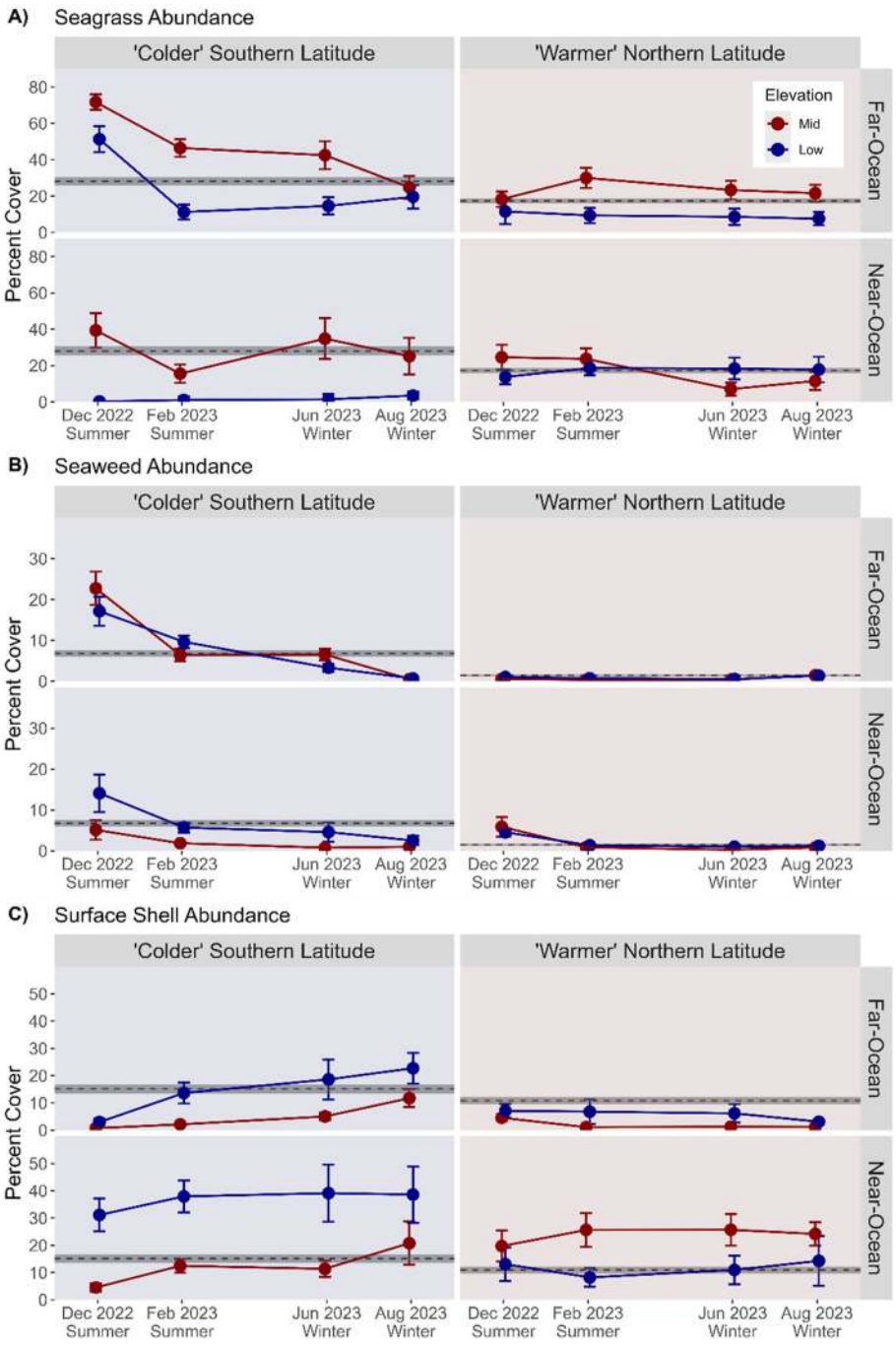


**Fig. 4. Abundance of foundation species from camera images.** Percent cover (mean ± 95 % CLs) of (A) seagrass, (B) seaweed, and (C) surface-deposited shells sampled across latitudes (northern vs. southern), sites (far vs. near ocean), elevation (mid vs. low), seasons (winter vs. summer), and intra-seasons (colder Dec 2022 & Aug 2023 vs. warmer Feb & Jun 2023). The horizonal dashed line is the overall mean ± 95 % CLs for each latitude (on average $n = 40$s).

drone and camera images, respectively, in ANOVA models for cover of surface shells (Tables 1 and 2). The test factor latitude was part of all significant interactions that explained >1 % of the SS; cover from drone images was affected by *Latitude* x *Site* x *Elevation* x *Intra-season* (1.1 %), *Latitude* x *Site* x *Elevation* (3.9 %), *Latitude* x *Elevation* (10.5 %) and *Latitude* x *Site* (4.6 %), and cover from camera images by *Latitude* x *Season* x *Intra-season* (1.1 %), *Latitude* x *Site* x *Elevation* (3.8 %), *Latitude* x *Elevation* (7.7 %) and *Latitude* x *Season* (1.4 %). The most important interactions highlight that shell abundances generally were higher in colder latitudes but prominently more so at low elevations (Figs. 3C and 4C). Main effects were again relatively similar between methods, where the most important significant factors for the drone images were *Site* (18.9 %), *Elevation* (3.5 %) and *Latitude* (1.0 % - although this factor was important in interactions), compared to *Site* (16.7 %), *Latitude* (3.8 %), *Elevation* (3.1 %) and *Season* (1.6 %) for the camera images. Shell cover was generally higher at near-ocean sites, the colder latitude estuaries, lower elevations and to a lesser extent during winter months (Figs. 3C and 4C).

*Shell density and length (alive/infaunal).* A total of 68.5 % of the SS was explained by the full ANOVA model over densities of live buried cockles (Table 3). Here densities were significantly affected by *Latitude* x *Site* x *Elevation* (2.6 %), *Latitude* x *Site* (16.6 %), *Site* x *Elevation* (5.8 %), *Latitude* x *Season* (4.8 %), and *Latitude* x *Elevation* (4.1 %), indicating that shell densities varied non-uniformly across most environmental

**Table 3**
**ANOVA for live Shells in quadrats.** Fixed permutational analysis of variance (perANOVA) of cockle shell density and shell length obtained from quadrat surveys. Significant *p-values* are boldfaced for alpha ≤0.01 for shell density (heterogeneous variances) and 0.01 for shell length (homogeneous variances, see Methods). Significant results with %SS ≥ 10 % and 1 % ≤ %SS < 10 % are highlighted in red and blue, respectively. Shading is based on actual %SS values prior to rounding ($N_{total}$ = 160, Df = 1 for all test factors, Df residuals = 128).

| | SHELL DENSITY | | | | SHELL LENGTH | | | |
|---|---|---|---|---|---|---|---|---|
| **Source of variation** | **SS** | **%SS** | **F** | **P** | **SS** | **%SS** | **F** | **P** |
| Latitude (Lat) | 36.77 | 15.2 | 61.80 | **0.000** | 0.112 | 0.3 | 1.53 | 0.219 |
| Site (Sit) | 1.62 | 0.7 | 2.72 | 0.102 | 7.799 | 24.1 | 106.61 | **0.000** |
| Elevation (Ele) | 0.09 | 0.0 | 0.16 | 0.694 | 2.824 | 8.7 | 38.61 | **0.000** |
| Season (Sea) | 22.31 | 9.2 | 37.49 | **0.000** | 2.743 | 8.5 | 37.49 | **0.000** |
| Intraseason (IntraSea) | 1.42 | 0.6 | 2.39 | 0.125 | 0.395 | 1.2 | 5.40 | **0.022** |
| Lat x Sit | 40.10 | 16.6 | 67.40 | **0.000** | 0.982 | 3.0 | 13.43 | **0.000** |
| Lat x Ele | 9.91 | 4.1 | 16.65 | **0.000** | 0.108 | 0.3 | 1.47 | 0.227 |
| Sit x Ele | 14.07 | 5.8 | 23.64 | **0.000** | 3.674 | 11.4 | 50.22 | **0.000** |
| Lat x Sea | 11.72 | 4.8 | 19.69 | **0.000** | 0.000 | 0.0 | 0.00 | 0.946 |
| Sit x Sea | 2.88 | 1.2 | 4.84 | 0.030 | 0.262 | 0.8 | 3.59 | 0.061 |
| Ele x Sea | 0.00 | 0.0 | 0.01 | 0.934 | 0.102 | 0.3 | 1.40 | 0.240 |
| Lat x IntraSea | 0.20 | 0.1 | 0.34 | 0.562 | 0.097 | 0.3 | 1.33 | 0.251 |
| Sit x IntraSea | 1.74 | 0.7 | 2.93 | 0.089 | 0.268 | 0.8 | 3.67 | 0.058 |
| Ele x IntraSea | 0.01 | 0.0 | 0.01 | 0.921 | 0.046 | 0.1 | 0.63 | 0.427 |
| Sea x IntraSea | 3.13 | 1.3 | 5.26 | 0.023 | 0.047 | 0.1 | 0.64 | 0.424 |
| Lat x Sit x Ele | 6.30 | 2.6 | 10.60 | **0.001** | 1.231 | 3.8 | 16.82 | **0.000** |
| Lat x Sit x Sea | 3.38 | 1.4 | 5.67 | 0.019 | 0.509 | 1.6 | 6.96 | **0.009** |
| Lat x Ele x Sea | 0.11 | 0.0 | 0.18 | 0.675 | 0.003 | 0.0 | 0.03 | 0.852 |
| Sit x Ele x Sea | 1.24 | 0.5 | 2.08 | 0.152 | 0.111 | 0.3 | 1.52 | 0.219 |
| Lat x Sit x IntraSea | 3.17 | 1.3 | 5.32 | 0.023 | 0.348 | 1.1 | 4.76 | **0.031** |
| Lat x Ele x IntraSea | 0.04 | 0.0 | 0.07 | 0.785 | 0.119 | 0.4 | 1.62 | 0.205 |
| Sit x Ele x IntraSea | 0.04 | 0.0 | 0.06 | 0.807 | 0.120 | 0.4 | 1.64 | 0.203 |
| Lat x Sea x IntraSea | 0.33 | 0.1 | 0.56 | 0.457 | 0.001 | 0.0 | 0.02 | 0.898 |
| Sit x Sea x IntraSea | 0.23 | 0.1 | 0.38 | 0.536 | 0.126 | 0.4 | 1.72 | 0.192 |
| Ele x Sea x IntraSea | 0.08 | 0.0 | 0.14 | 0.707 | 0.006 | 0.0 | 0.08 | 0.779 |
| Lat x Sit x Ele x Sea | 0.50 | 0.2 | 0.84 | 0.361 | 0.034 | 0.1 | 0.46 | 0.499 |
| Lat x Sit x Ele x IntraSea | 1.50 | 0.6 | 2.52 | 0.115 | 0.004 | 0.0 | 0.06 | 0.810 |
| Lat x Sit x Sea x IntraSea | 0.00 | 0.0 | 0.00 | 0.980 | 0.197 | 0.6 | 2.69 | 0.103 |
| Lat x Ele x Sea x IntraSea | 1.71 | 0.7 | 2.88 | 0.092 | 0.002 | 0.0 | 0.02 | 0.882 |
| Sit x Ele x Sea x IntraSea | 0.72 | 0.3 | 1.21 | 0.274 | 0.625 | 1.9 | 8.54 | **0.004** |
| Lat x Sit x Ele x Sea x IntraSea | 0.15 | 0.1 | 0.25 | 0.620 | 0.105 | 0.3 | 1.43 | 0.234 |
| Residuals | 76.16 | 31.5 | | | 9.364 | 28.9 | | |

gradients. Among the main effects, only *Latitude* (15.2 %) and *Season* (9.2 %) were significant, suggesting that shell densities generally were higher in southern latitudes and warmer seasons (Fig. 5A). Finally, the ANOVA model for shell length explained 71.1 % of the SS (Table 3). Shell length was significantly affected by 6 significant interactions (all explaining >1 % of the SS, including *Site* x *Elevation* x *Season* x *Intra-season* (1.9 %), *Latitude* x *Site* x *Elevation* (3.8 %), *Latitude* x *Site* x *Season* (1.6 %), *Latitude* x *Site* x *Intra-season* (1.1 %), *Site* x *Elevation* (11.4 %) and *Latitude* x *Site* (3.0 %), again indicating non-uniform responses across environmental gradients. Among the main effects, *Site* was most important (24.1 %), followed by *Elevation* (8.7 %), *Season* (8.5 %), and *Intra-season* (1.2 %). Shells were generally larger at near-ocean sites, lower elevations, and during winter (Fig. 5B).

### 3.3. Correlations

The correlations between cover of shells and seagrass were significant and negative across methods and seasons (Fig. 6A, $p < 0.001$) being stronger in summer for both drone and camera images ($R_{Spearman} = -0.51$ vs. $-0.58$) compared to winter ($-0.27$ vs. $-0.31$). Correlations between seaweed and seagrass were not significant in summer but negative (albeit weak) in winter for both drone ($-0.09$) and camera

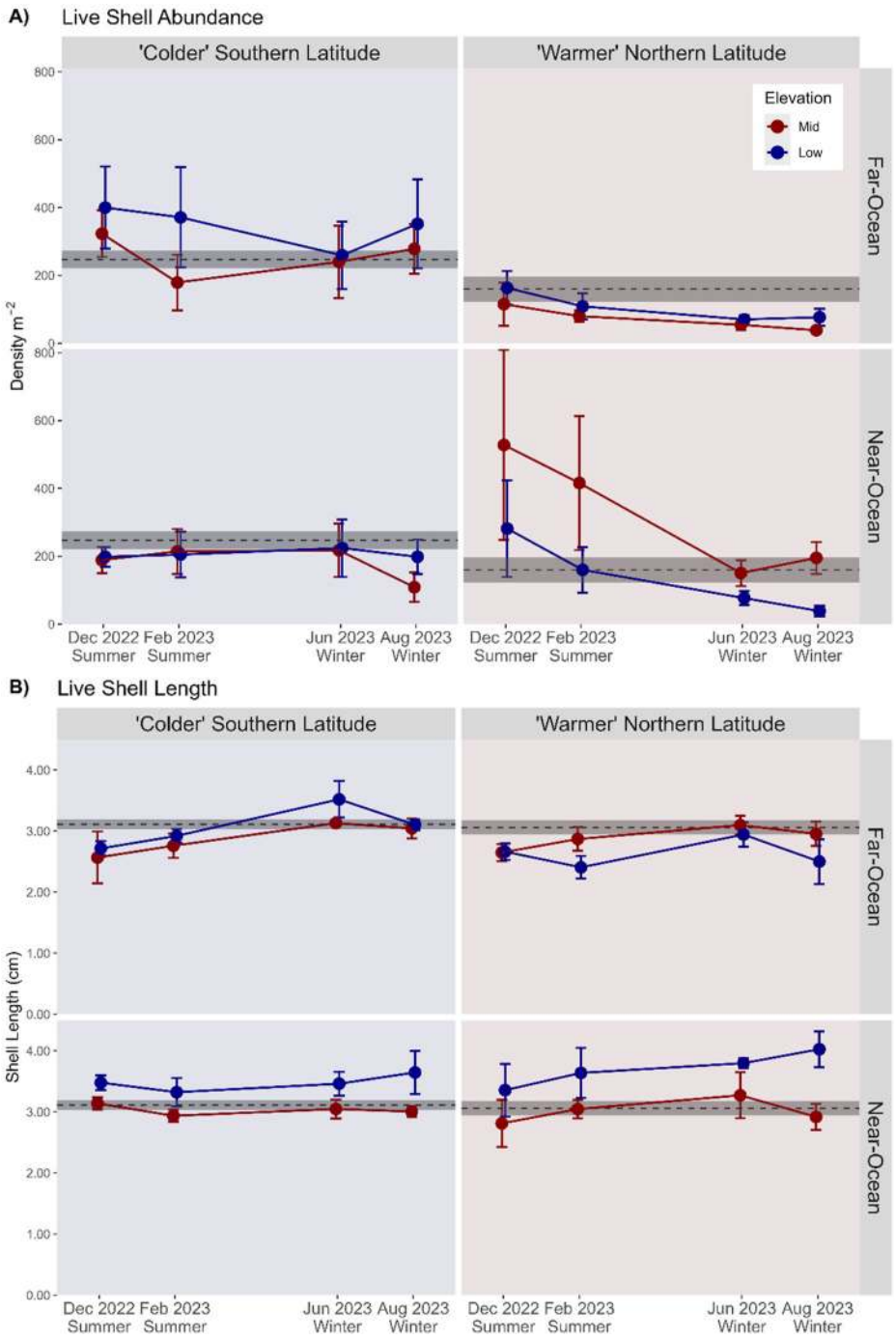


**Fig. 5. Abundance and sizes of live cockles from quadrats**. Mean (±95 % CLs) densities of live cockles (A) and their shell lengths (B) obtained from quadrats (0.0625 $m^2$), sampled across latitudes (northern vs southern), sites (far vs. near ocean), elevation (mid vs. low), seasons (winter vs. summer), and intra-seasons (colder Dec 2022 & Aug 2023 vs. warmer Feb & Jun 2023). The horizonal dashed line is the overall mean ± 95 % CLs limits for each latitude ($n = 5$).

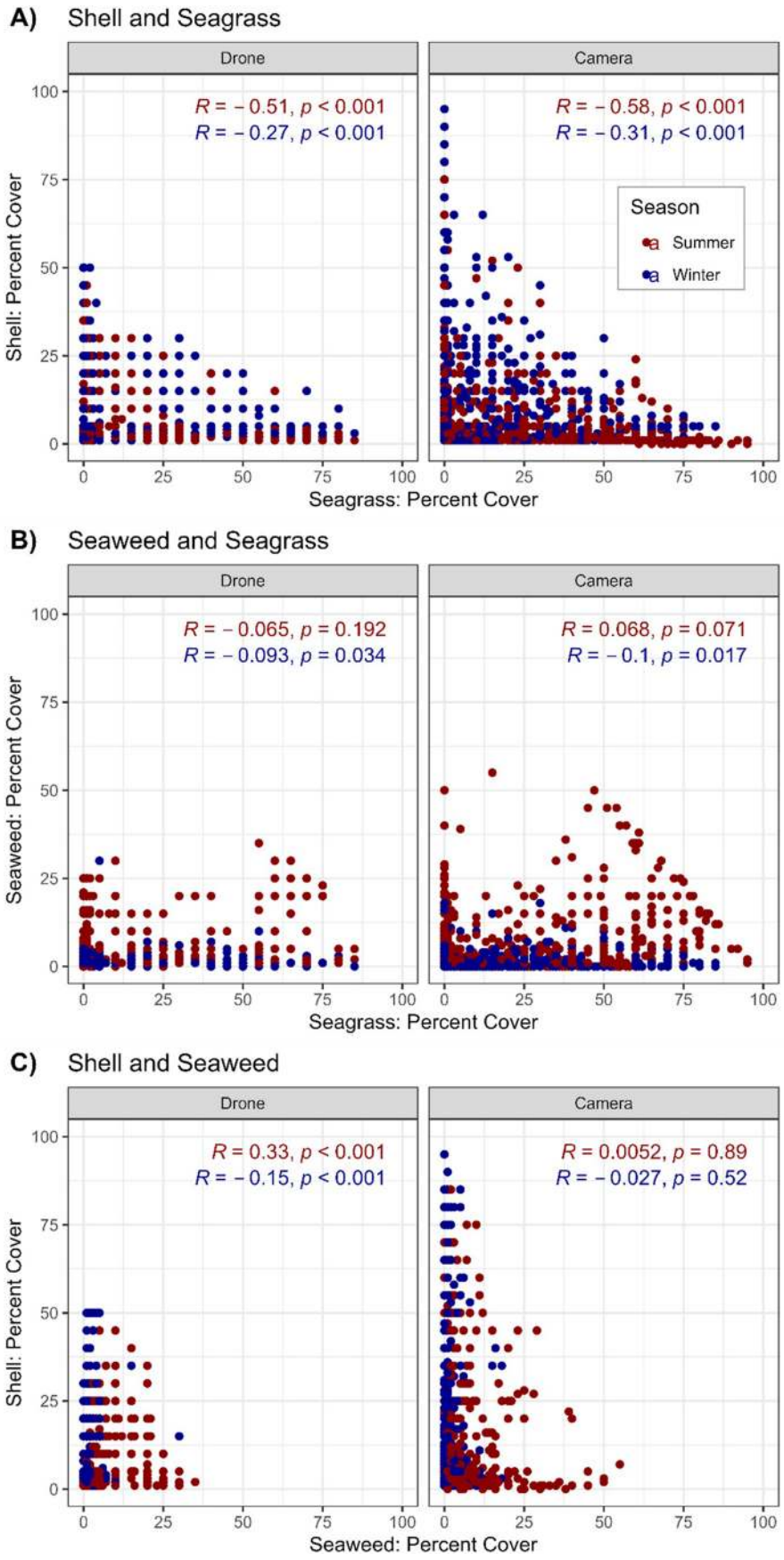


**Fig. 6. Correlations between foundation species.** Spearman's rank correlation between percent cover of (A) surface deposited shells and seagrass, (B) seaweed and seagrass and (C) shell and seaweed, analyzed for camera and drone images in both summer (red) and winter (blue). $R$ = Spearman's correlation coefficient. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(−0.10, $p < 0.05$, Fig. 6B) images. Finally, we found no associations between cover of shells and seaweeds for camera images ($p = 0.89$ and 0.52 for summer and winter, respectively) but a moderate positive correlation in summer (0.33, $p < 0.001$) and a weak negative correlation in winter (−0.15, $p < 0.001$, Fig. 6C) for drone images.

## 4. Discussion

Here we showed that estuarine tidal flats, which are often describe as "bare" (Ramus et al., 2017; Dissanayake et al., 2018; Thomsen et al., 2019), can support habitat heterogeneity resulting from co-occurring habitat-forming foundation species (FS). Across the 32 sampled estuarine environments in the South Island of New Zealand, we found widespread and overlapping distributions of seagrasses (*Zostera muelleri*), seaweeds (*Ulva* and *Gracilaria*), and surface-deposited shells, consistently forming multi-FS assemblages thereby increasing structural (and likely also functional) habitat heterogeneity. While most previous studies have focused on heterogeneity arising from conversion of bare habitats to a single type of habitat-forming foundation species (Dayton, 1972; Stachowicz, 2001; Ellison et al., 2005; Ellison, 2019; Wernberg et al., 2024), our results align with more recent work showing the importance of co-occurring and functionally complementary FS (Altieri et al., 2007; Yakovis et al., 2008; Angelini et al., 2011; Thomsen et al. 2013, 2018). These findings may also lead to an improved understanding of biodiversity, secondary production, and resilience in estuarine systems, especially under changing environmental conditions (Gustafsson and Boström, 2011; Bishop et al., 2022).

### 4.1. Seagrass abundance

In contrast to the extensive and dense subtidal seagrass meadows commonly found in other parts of the world, *Zostera muelleri* in New Zealand estuaries typically forms smaller, sparse patches with current and historical low percent cover (Battley et al., 2011; Lundquist et al., 2018). Our results indicate that seagrass cover was typically less than 30 %. The relatively low abundance of seagrasses in these estuaries may reflect the species' resilience and adaptation to harsh conditions, such as fluctuating salinity, temperature, desiccation, grazing pressure, and high sediment loading (Dos Santos et al., 2013; Macreadie et al., 2014; Clemente et al., 2023). Despite its relatively low abundance, *Z. muelleri* plays a crucial role in supporting a variety of ecosystem functions and services, including stabilizing sediments, providing habitat and nursery grounds for many marine species, and enhancing biodiversity (Battley et al., 2011; Lundquist et al., 2018; Pullen et al., 2022; Dalby et al., 2023) and is therefore considered a foundation species in New Zealand estuaries. We observed greater seagrass abundance in colder southern estuaries compared to warmer northern estuaries, perhaps reflecting the species' adaptation to cooler water temperatures. Previous studies have shown that reproductive effort, such as flowering, is more favorable under colder conditions, promoting persistence and growth (Lekammudiyanse et al. 2023, 2024). Alternatively, genetic studies in New Zealand indicate that *Z. muelleri* populations in different latitudinal regions may have adapted to local habitat conditions, potentially explaining higher abundance in specific areas, regardless of regional temperature profiles (Jones et al., 2008). Additionally, sites farther from ocean openings exhibited higher seagrass cover, likely due to reduced salinity stress, clearer waters and stronger tidal flushing, which create more stable and less turbid water conditions (Fonseca and Bell, 1998; Sharma et al., 2016; Maxwell et al., 2017). Seagrass cover may also be lower in the low tidal zone as sediments are more silty and anoxic, and light levels lower (Heiss et al., 2000; Kohlmeier et al., 2014; Bulmer et al., 2016). The minimal temporal variation in seagrass cover suggests that *Z. muelleri* is tolerant of fluctuating conditions and relies on vegetative reproduction rather than seasonally-controlled seed production (Conacher et al., 1994; Macreadie et al., 2014). However, minor discrepancies between seagrass cover observed through drone images and camera surveys (*ca.* 3 % average cover difference) suggest methodological limitations that could influence data interpretation. Drone imagery may not detect small patches with sparse densities compared to ground-based camera surveys. Conversely, drones capture larger-scale patterns and can encompass both vegetated and unvegetated areas that camera surveys might under-sample due to their limited spatial extent.

### 4.2. Seaweed abundance

Seaweeds are often regarded as a nuisance in estuaries because dense mats of nutrient-enriched algal blooms can smother benthic communities and degrade water quality (Hauxwell et al., 2001; Piazzi et al., 2007; Deudero et al., 2011; Thomsen et al., 2012; Ceccherelli et al., 2014). However, our findings suggest that *Ulva* and *Gracilaria* at our study sites mainly were present as small, scattered patches with overall much lower cover than seagrass (average of 4 % in both drone and camera surveys). The low cover suggests that seaweeds in these estuaries may serve a different ecological role, potentially acting as supplementary habitat structures rather than as competitors for space, light and nutrients (Thomsen et al., 2012). Seaweeds were often found entangled within seagrass blades or attached to shells, suggesting that estuarine seaweeds can be facilitated by other foundation species (Clemente and Thomsen, 2023, 2024). While algal blooms or green tides do occur in New Zealand estuaries and can be toxic to aquatic life (Nelson et al., 2015; Siciliano et al., 2019; Zabarte-Maeztu et al., 2023), the seaweeds observed in this study were more ephemeral and more influenced by seasonal and monthly variation rather than spatial test factors (Figs. 3B and 4B). The greater abundance of seaweeds in summer compared to winter is likely driven by rapid growth during warmer temperatures, higher light availability, and increased nutrient levels (Phillips and Hurd, 2000; Nelson et al., 2015; Wilson et al., 2015; Green-Gavrielidis and Thornber, 2022). In addition to these seasonal drivers, latitudinal variation in abundance appears to be shaped by site-specific factors, such as nutrient availability, sedimentation, and hydrodynamic conditions, rather than by regional thermal gradients alone (Miller et al., 2020; Véliz et al., 2020; Hadiyanto et al., 2024). The higher seaweed abundance observed at lower tidal elevations may reflect reduced desiccation stress and perhaps less disturbances from currents and storm-waves, and thereby increased accumulations of fragments on and around shells and seagrass leaves (Bracken et al., 2011; Thomsen et al., 2015). Sites farther from estuary mouths exhibited higher seaweed cover, likely due to a combination of reduced osmotic stress, increased nutrient retention, clearer waters and more abundant seagrass and cockles to attach to and entangle around, as observed in some estuarine *Ulva* populations (Aldridge and Trimmer, 2009; Shaw et al., 2018). Overall, this suggests that the seaweed at our study sites, generally complement other FS in supporting slightly more and/or different invertebrate communities (Holmquist, 1997; Thomsen et al., 2016a; Siciliano et al., 2019; Vieira et al., 2020), rather than posing a significant threat to local seagrass beds or bivalves. The similar cover estimates between the drone and camera methods suggest these seaweeds are scattered relatively evenly across the surveyed environments, which allows for reliable detection across scales. The generally low percent cover also highlights the need to reconsider assumptions about their nuisance effect on estuarine ecosystems in this region.

### 4.3. Shell abundance

Surface-deposited shells, predominantly from the bivalve *Austrovenus stutchburyi*, were a defining feature of the sampled estuarine environments, occurring in 99.5 % of images. Despite their ubiquity, dead shell cover remained low (9 % in drone images and 13 % in camera images). Live infaunal *A. stutchburyi* shells, on the other hand, showed 100 % occurrence across all quadrats, with densities and shell lengths influenced by complex interactions among environmental gradients.

These findings reflect the combined complex effects of site-specific factors – like currents, waves, food availability, predation, sediment grain sizes, turbidity, salinity and sedimentation - and broader seasonal and latitudinal patterns. Similar to seagrass observations, discrepancies between methods may reflect sampling biases, particularly in detecting aggregates or patches of FS or limitations in resolving finer details. The greater abundance of *A. stutchburyi* dead and live shells in estuaries at southern latitudes could reflects temperature effects, or alternatively site-specific factors such as unmeasured co-varying sediment dynamics or historical population densities (Thrush et al., 1996). Seasonal patterns showed differing trends between live and dead shells. Higher densities of live shells were observed in summer, probably because warmer seasons enhance planktonic primary production and therefore food availability, which elevates population growth. By contrast, the slightly higher cover of dead shell in winter could result from seasonally-controlled mortality of *A. stutchburyi,* new exposure of previously buried shells from winter storms, or simply because reduced cover of seaweed and seagrass may make it easier to detect the surface deposited shells from the images (Norkko et al., 2006; Green et al., 2009). Additionally, higher cover of live and dead shells at lower tidal elevations may be linked to longer submersion time, longer time for suspension feeding, reduced desiccation stress, and/or because channel currents can concentrate dead shells and provide food for live cockles (Wiedemann, 1972; Byers et al., 2015). The widespread presence of dead shells indicates they may be important contributors to increase habitat heterogeneity, as documented in Manukau Harbour on the North Island of New Zealand (were ca. 50 % of samples had accumulations of dead bivalve shells) (Grange, 1979) or near the Hikurangi Margin tectonic (with some areas containing massive accumulations) (Greinert et al., 2010). Our study thereby support reviews that have suggested that dead foundation species have important legacy effects on biodiversity and community structures (Gutiérrez et al., 2003; Saldaña et al., 2024). For instance, dead shell deposits can create microhabitats for sessile species like barnacles and algae (e.g., *Ulva* or *Gracilaria*) as well as mobile species, like snails, limpets, and sea anemones (Clemente and Thomsen, 2024). Still, the ecological role of dead shell deposits, particular within seagrass beds, is poor studies and warrant new research.

### 4.4. Co-occurrences among the three foundation species (FS)

Our study demonstrates that estuarine FS rarely exist in isolation, with all three FS (seagrasses, seaweeds, shells) co-occurring in over 69 % of drone images and 50 % of camera images. This result highlights the importance of studying co-occurring FS rather than focusing solely on single-species, particular because co-occurring FS typically enhance biodiversity and ecosystem stability (Stachowicz, 2001; Thomsen et al., 2018). Examples from other ecosystems, such as co-occurring corals and sponges (Slattery and Lesser, 2021), mangroves and seagrass (Alfaro, 2006; Jones et al., 2021), and mangroves and corals (Stewart et al., 2022), similarly highlight how FS interactions shape community structure and enhance ecosystem functions. In our study, co-occurrences among seagrass, seaweed, and bivalve shells suggest that estuarine habitats are more complex than often assumed. By creating habitat heterogeneity, these FS are likely key contributors to estuarine community structure and productivity. The co-occurrence patterns may be driven by ecological interactions arising from their functional traits, like competition for nutrients, light, and space between seagrasses and seaweeds (Dumay et al., 2002; Irlandi et al., 2004; Stafford and Bell, 2006; Thomsen et al., 2012). However, our correlation analysis suggests inconsistent competitive interactions over time, perhaps partly because we generally found low seaweed cover (4 %), i.e., competition from seaweed is likely weak. We speculate that, in our study system, even if these seaweed blooms, negative impact on seagrasses is likely also ephemeral because *Z. muelleri* may recover rapidly through vegetative regeneration and recolonization from drifting ramets (Dos Santos et al., 2013; Macreadie et al., 2014; Stafford-Bell et al., 2015; Matheson et al., 2017). Conversely, seagrasses may facilitate seaweed through physical attachment, as suggested by field observations in our study sites, where drift seaweed is often found entangled in seagrass blades (Holmquist, 1997; Irlandi et al., 2004).

By comparison, the effects of scattered dead or live infaunal shells on seagrasses and seaweed are less understood. The negative correlations between seagrass and surface shells observed here indicate that shells may inhibit seagrass growth, potentially by altering sediment conditions, such as increasing sulfide concentrations, or through competition for space (Vinther and Holmer, 2008; Wagner et al., 2012). High shell densities may also physically smother seagrass blades, and inhibit their growth and photosynthesis (Zhu et al., 2007). Furthermore, seagrass roots and rhizomes modify below-ground sediment characteristics, potentially inhibiting growth of bivalve shells (Gribben and Wright, 2014) and ultimately reduce the likelihood of them accumulating on the sediment surface. Interestingly, shell and seaweed cover were positively correlated in summer but (weakly) negatively correlated in winter. Surface shells were relatively stable over time, so this variability likely reflects changes in seaweed abundance, likely driven by changes in nutrient availability, temperature, storminess, and herbivory, which strongly affect seaweed growth, reproduction and decomposition (Raffaelli et al., 1998; Yamaguchi, 2010; Zhang et al. 2016, 2020). Furthermore, warmer temperatures during summer may underpin positive interactions between seaweed and bivalve shells by promoting recruitment and attachment of seaweed to shell surfaces (Clemente and Thomsen, 2023).

### 4.5. Methodological considerations

The differences between drone and camera survey results highlight complementary strengths and limitations of each method. Drone surveys cover larger spatial extents, facilitating detection of landscape-scale patterns and co-occurrences across broader scales (Hamad et al., 2022; Ventura et al., 2023). However, drones may lack the resolution to identify fine-scale details, such as individual shells small seaweed entangled within seagrasses or small sparse patches of small seagrass leaves. In contrast, camera surveys offer higher-resolution imagery, allowing for detection of these aforementioned fine-scale details, but are limited in spatial coverage and may miss broader landscape patterns (Salas-Aguilar et al., 2017). This trade-off underscores the importance of using complementary methods to capture the complexity of estuarine FS across scales. However, a key limitation of image-based surveys (from cameras, drones or satellites) is that they only record 2D-surface canopies (up to 100 % cover), overlooking vertical layering and sub-canopy species. This limitation will generally bias results toward negative correlations (if there is 100 % cover of seaweed, there can be no cover of shells or seagrass) (Koedsin et al., 2016; Beisiegel et al., 2017; Martin et al., 2020). As such, inferences about FS interactions should be made cautiously, acknowledging these methodological constraints. Addressing these limitations through methods that allow for sub-canopy detection is crucial to avoid these biases in ecological interpretations (which can only be done by physically removing the top canopy). Despite this limitation we nevertheless observed co-occurrences to be common at all our study sites. Furthermore, by integrating drone and camera surveys with very different sample extent and grains, researchers can reduce sampling biases, enhance data resolution, and develop a more comprehensive understanding of co-occurrence patterns (Koedsin et al., 2016; Hamad et al., 2022). Future advances in remote sensing technology, such as increasingly high-resolution imagery and application of Artificial Intelligence (AI) for automated image analysis, is expected to improve accuracy and efficiency of FS monitoring in the near future (Ditria et al., 2022; Goodwin et al., 2022). Finally, using standardized protocols across studies and regions will facilitate comparisons and broader applications of these methods in estuarine and coastal studies.

### 4.6. Implications for community facilitation

Our findings have important implications for understanding both direct and indirect facilitation among FS in estuarine ecosystems. The co-occurrence of multiple FS enhances habitat heterogeneity, creating a mosaic of microhabitats that can shape community structure by providing niches for a variety of species (Altieri et al., 2007; Thomsen et al., 2010). This elevated structural complexity among estuarine FS can result in facilitative interactions that supports higher trophic levels, increase biodiversity, and enhance secondary production (Bruno et al., 2003). Direct facilitation occurs when one FS positively influences another. For example, seagrasses can facilitate seaweed by providing attachment sites, while shells may serve as substrates or refuges for seaweed attachment. Indirect facilitation, on the other hand, arises from the modification of environmental conditions. For instance, water filtration by bivalves can improve conditions for seaweed, which in turn create habitats for third-order inhabitants such as small crabs, snails, copepods, and amphipods. Recognizing and understanding these facilitative interactions is critical for the conservation and management of aquatic resources. Protecting and restoring multi-FS assemblages can amplify positive ecological effects, enhance ecosystem services, and bolster the resilience of estuarine ecosystems in the face of environmental stressors.

## 5. Conclusions

This study demonstrates foundation species (here seagrasses, seaweed, and shells) co-occur across many estuarine environments in the South Island of New Zealand, to increase habitat heterogeneity and likely also biodiversity. Shells were most ubiquitous, whereas seagrass was most abundant and consistently co-occurred with shells and/or seaweed. Spatial factors, such as latitude, site proximity to the ocean, and tidal elevation, were primary drivers of FS abundances, while temporal factors mainly affected seaweed abundance and live shell densities. Test results varied slightly between analysis from drone and camera surveys, highlighting the importance of using complementary methods to achieve robust ecological assessments of abundances. For example, negative correlations were consistently observed between seagrass and both shells and seaweed, whereas positive correlations between shells and seaweed shifted from negative in winter to positive in summer. Furthermore, the ubiquity of dead shell deposits underscores the need to study their potential biogenic legacy effects and their roles in structuring ecological communities. Future studies should adopt experimental approaches to elucidate the mechanisms underlying co-occurring FS interactions and assess the functional significance of multi-species assemblages. Finally, these findings have potential applications for guiding future research and conservation efforts, including protection of aquatic resources, promotion of blue carbon ecosystems, identification of biodiversity hotspots, and the design of nature-based solutions.

## CRediT authorship contribution statement

**Ken Joseph E. Clemente:** Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **Mads S. Thomsen:** Conceptualization, Formal Analysis, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107150.

## Data availability

Data will be made available on request.

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