





ARTICLE

Coastal and Marine Ecology

Changing intra- and interspecific interactions across sedimentary and environmental stress gradients

Emily J. Douglas¹  | Judi Hewitt^{1,2}  | Andrew M. Lohrer¹  |
Fabrice Stephenson¹ 

¹National Institute of Water & Atmospheric Research, Hamilton, New Zealand

²Department of Statistics, University of Auckland, Auckland, New Zealand

Correspondence

Emily J. Douglas
Email: emily.douglas@niwa.co.nz

Present address

Fabrice Stephenson, School of Science, University of Waikato, New Zealand.

Funding information

National Institute of Water and Atmospheric Research (NIWA) Coast and Oceans SSIF Funding, Grant/Award Numbers: COME2101, COME2201

Handling Editor: Max C. N. Castorani

Abstract

Intensifying land use and accelerated erosion has resulted in increased delivery and deposition of fine terrestrially derived sediment to coastal ecosystems, increasing sediment mud content in estuarine ecosystems. This change in the sedimentary environment is known to have negative consequences for ecosystem functioning. Yet indirect and cyclical relationships between species and the environment are rarely investigated, despite being crucial for understanding ecosystem resilience. We investigate changes in intra- and inter-specific interactions between two key intertidal species (*Austrovenus stutchburyi* and *Macomona liliana*) with different but overlapping environmental preferences. We use a large dataset spanning 29 estuaries and 0%–87% mud content to predict the effects of increases in mud. We observed important changes in feedback loops between *Austrovenus* recent recruits, older individuals, and sediment shell content, and between *Macomona* and chlorophyll with increasing stress (mud). These loops show different characteristics in the high and low mud content ecosystems and are not apparent in moderate mud. Increases in the number of paths and weaker/more variable relationships between low and moderate mud also occurred. Thus, our moderate (12%–25%) mud content model may be encompassing a transition point in ecosystem dynamics where interaction networks break down and shift to an alternate state.

KEYWORDS

Austrovenus, estuarine, *Macomona*, mud, resilience, soft sediment, structural equation modeling

INTRODUCTION

The properties of coastal marine sediments are known to influence the structure and dynamics of benthic soft sediment ecosystem communities (Anderson, 2008; Ellis

et al., 2015; Gray, 2002; Jacquot et al., 2018; Rhoads & Germano, 1982; Rowden et al., 2012). For example, sediment grain size often correlates with suspension and deposit feeder abundance, with deposit feeders more prevalent in depositional areas with muddy sediment

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

where sediment organic matter concentrations are high enough to support their nutritional requirements (Peterson, 1991; Pratt et al., 2015; Probert, 1984). However, depositional zones with fine bed sediments may be less suitable for suspension feeders (Bell et al., 2015; Topçu et al., 2019). The gills and feeding structures of suspension feeders can become clogged with suspended fine sediments (smothering or starving them; Bishop & Peterson, 2006) and high rates of sediment accretion can bury suspension feeders (interfering with their access to overlying water; Lohrer et al., 2006). The shifts in macrofaunal communities that occur across sand-to-mud sedimentary gradients are associated with changes in key benthic rates and processes (organic matter degradation rates, nutrient regeneration/removal, and microphytobenthic primary production) that contribute to the health and functioning of coastal ecosystems (Norkko et al., 2006; Pratt et al., 2013; Thrush et al., 2012).

Shifts in intertidal soft sediment communities corresponding to changing sedimentary environments have been documented in many New Zealand estuaries (Swales et al., 2020; Thrush et al., 2004). Intensifying land use and accelerated erosion of landscapes has resulted in increased delivery and deposition of fine terrestrially derived sediment to coastal ecosystems resulting in the “muddying” of estuaries (Thrush et al., 2004). Increasing sediment mud content (silt and clay particles <63 μm) is a key stressor in estuarine ecosystems and is known to have negative consequences for ecosystem functioning (Pratt et al., 2013; Rodil et al., 2011), biodiversity (Lohrer, Thrush, Hewitt, et al., 2004; Rodil et al., 2013), animal behavior (Hohaia et al., 2013; Woodin et al., 2012), and resilience to other stressors (Douglas et al., 2018). As the physical environment changes with increasing stressors, so too does the availability of food and other factors affecting interactions within and among species. Additionally, different species and life stages respond differently to increasing stressors. For example, filtration rates of suspension feeders can be greater in muddy environments to compensate for higher inorganic:food particle ratios in the bottom water at these sites due to the higher concentrations of suspended fine sediments in muddy areas (Armsworthy et al., 2001). Elevated filtration rates are energetically costly and can influence physiological condition, growth rate, reproductive output, and population dynamics (Ellis et al., 2002; Hawkins et al., 1998).

Two key bivalve species that can co-occur in intertidal estuarine soft sediment habitats throughout New Zealand are the suspension-feeding venerid bivalve *Austrovenus stutchburyi* (hereafter *Austrovenus*) and the deposit-feeding tellinid bivalve *Macomona liliana* (hereafter *Macomona*). Their abundances are generally inversely correlated (Stephenson et al., 2022), with habitats dominated by one or the other species. However, *Austrovenus* and *Macomona*

are not strictly sand-loving or mud-loving taxa, respectively, (co-occurring across a 0%–80% sediment mud content range in New Zealand estuaries), suggesting that biotic interactions between them may play a role in their patchwork distributions (Stephenson et al., 2022). Both species are stressed by increasing sediment mud content and, for both species, small individuals are more sensitive to fine sediment deposition than larger conspecifics (Lohrer, Thrush, Hewitt, et al., 2004). We predict interspecific and adult–juvenile interactions between *Austrovenus* and *Macomona* to matter most outside of their optimal environmental limits (i.e., when they are under more stress).

By studying existing habitats and communities across a spectrum of sediment mud content, we can gain insights into how intra- and interspecies interactions change with sedimentary environment and analyze the potential effects of estuarine muddying, using ecosystem interaction networks and a space-for-time substitution. Space-for-time substitution analyses use spatial sampling across existing gradients to understand longer term temporal processes (Blois et al., 2013; Pickett, 1989), in this case, estuarine sedimentation that occurs over decades or centuries. Interaction networks are a powerful tool in ecology, allowing visualization of the many complex and interrelated biotic and abiotic components of ecosystems (Bulmer et al., 2022). Mechanisms of change are often difficult to pinpoint, but with interaction network tools we can begin to interpret positive and negative feedbacks, and the multiple indirect effects that small changes can have on ecosystem components and processes (Grace et al., 2010). Structural equation models (SEMs) are a type of interaction network that can be used to generalize complicated heterogeneous ecosystems, link ecological theory with real data (Grace et al., 2010), and may be used to assess ecosystem resilience or integrity (Capmourteres & Anand, 2016; Mora, 2017; Thrush et al., 2012).

Unidirectional relationships between species, communities, and environment are commonly investigated, but feedbacks (cyclical relationships) are rarely accounted for. Yet these feedbacks may be crucial for understanding resilience, especially if they vary ontogenetically (with life stage). Many species show ecological plasticity and exist across a range of environmental conditions, but the functional role of species may differ depending on environmental setting (e.g., Needham et al., 2010). Variations in body size, feeding, and behaviors of adult and juvenile conspecifics affect their role in an ecosystem. For example, juveniles may be more vulnerable to predation, and their functional influence (as habitat modifiers, competitors, predators, grazers, etc.) is generally less than larger sized adults (Norkko et al., 2013). These asymmetries shape the structure and dynamics of communities (de Roos, 2021). Asymmetric patterns in biotic interactions can help

explain patterns in species abundance and distributions (Stephenson et al., 2022), and at the species level, positive relationships and feedbacks between adult and juvenile conspecifics are central to maintenance of populations. Analyzing these relationships, along with other ecosystem components that influence them, can help us to understand or predict how populations and communities change in response to changing environmental conditions. Differences in relationships and feedbacks affect the functioning of the ecosystem as a whole and are expected to manifest as differences in interaction network architecture (Thrush et al., 2020).

Austrovenus and *Macomona* are common throughout New Zealand estuaries with latitudinal distributions spanning -35.7° and -46.6° (Mangan et al., 2020). These species have important roles in local ecosystem functioning through their positive influence on biodiversity, benthic-pelagic coupling, and habitat alteration (Lohrer et al., 2012; Rullens et al., 2019; Thrush et al., 2003). Small *Macomona* (≤ 5 mm) typically live in the top 2 cm of the benthos, while larger individuals (> 5 mm) occur deeper (up to 10 cm) and surface feed with a long inhalant siphon (Hewitt, Legendre, et al., 1997). With *Austrovenus*, both the smaller (< 5 mm) and larger (≤ 5 mm) individuals live in the top 2 cm of the sediment but exhibit differences in patch distribution and behaviors according to size (Hewitt, Legendre, et al., 1997). These species are known to interact, and their interactions are known to change depending on life stage and environmental context. For example, through surface deposit feeding activity, adult *Macomona* can hinder settlement of juvenile *Austrovenus* (and possibly juvenile conspecifics), but only at high densities (Thrush et al., 2000; Thrush, Hewitt, et al., 1996). Similarly, when *Austrovenus* occur at very high densities, they form a dense shell-to-shell layer on the surface sediment, which may disrupt the feeding or completely exclude *Macomona*.

This study aimed to investigate intra- and interspecific interactions, as well as species–environment interactions of two key intertidal species, *Austrovenus* and *Macomona*, across different sedimentary environments using ecosystem interaction networks modeled using SEMs. We use a dataset spanning multiple sites (29 estuaries, 5.3° latitude and 3.9° longitude) with a broad environmental gradient in mud content (0%–87%) to create models that can suggest, based on space-for-time substitution, effects of future increases in mud. We predict that interaction network structure will change significantly across the 0%–87% gradient in bed sediment mud content and that networks under high mud (high stress) will be simpler (fewer significant paths). Further, we predict that inter- and intraspecies interactions will be stronger with increasing stress.

METHODS

Data compilation

Data were compiled from 18 separate datasets from research studies or monitoring programs collected between 2000 and 2019, spanning over 29 different estuaries (Figure 1; Appendix S1: Table S1). These datasets included measures of macrofaunal community, sediment grain size, microphytobenthic biomass, and sediment organic matter content data, which were sampled and measured in a consistent manner across the different datasets.

Macrofaunal community samples were collected using multiple replicate cores (13-cm diameter, 15-cm depth) at each site (ranging from 3 to 12 replicate cores depending on the study/monitoring dataset). Materials collected in the cores were sieved (500- μ m mesh) and preserved in 50% isopropyl alcohol until analysis. Samples were stained with Rose Bengal and all individuals were counted and identified to the lowest possible taxonomic resolution (usually species level). In this study, abundances of two size categories of the two key shellfish species were quantified for analysis: pre-recruits (< 5 mm) and post-recruits (≥ 5 mm) of *A. stutchburyi* and *M. liliiana*. The 5-mm size cut-off was based on the propensity of these bivalves for secondary dispersal after settling to the benthos. *Macomona* and *Austrovenus* < 5 mm (i.e., pre-recruits) are highly mobile as they choose their adult habitat (Cummings et al., 1993, 1995; Hewitt, Pridmore, et al., 1997; Lundquist et al., 2004; Pridmore et al., 1991). In contrast, *Macomona* and *Austrovenus* > 5 mm (i.e., post-recruits) are generally greater than one year old (Roper et al., 1992a) and sedentary (Hewitt, Pridmore, et al., 1997), having occupied their adult habitat. Hereafter, for brevity, the two size classes are referred to as “juveniles” and “adults.”

Sediment properties and microphytobenthic biomass samples were collected (3 cores pooled, 2.3-cm diameter and 2-cm depth), stored in the dark, on ice, transported to the laboratory, and frozen until analysis. Amalgamating sediment core samples is standard practice for New Zealand estuarine sediment sampling to save time and expense because grain size does not typically vary much among true replicates at a site. Wet sieving (after digestion in 6% hydrogen peroxide for 48 h) was used to measure the cumulative percentage mass of sediment size fractions (Gatehouse, 1971). For this study, shell (Shell, % > 2 mm) and mud (Mud, % < 0.063 mm) fractions were used. The > 2 mm sediment fraction is referred to as gravel according to the Wentworth scale; however, in these estuaries, it is almost entirely composed of bivalve shell material, which has a significant influence on macrofaunal community structure (Ellingsen et al., 2007; Thrush et al., 2013). We chose to use both mud and

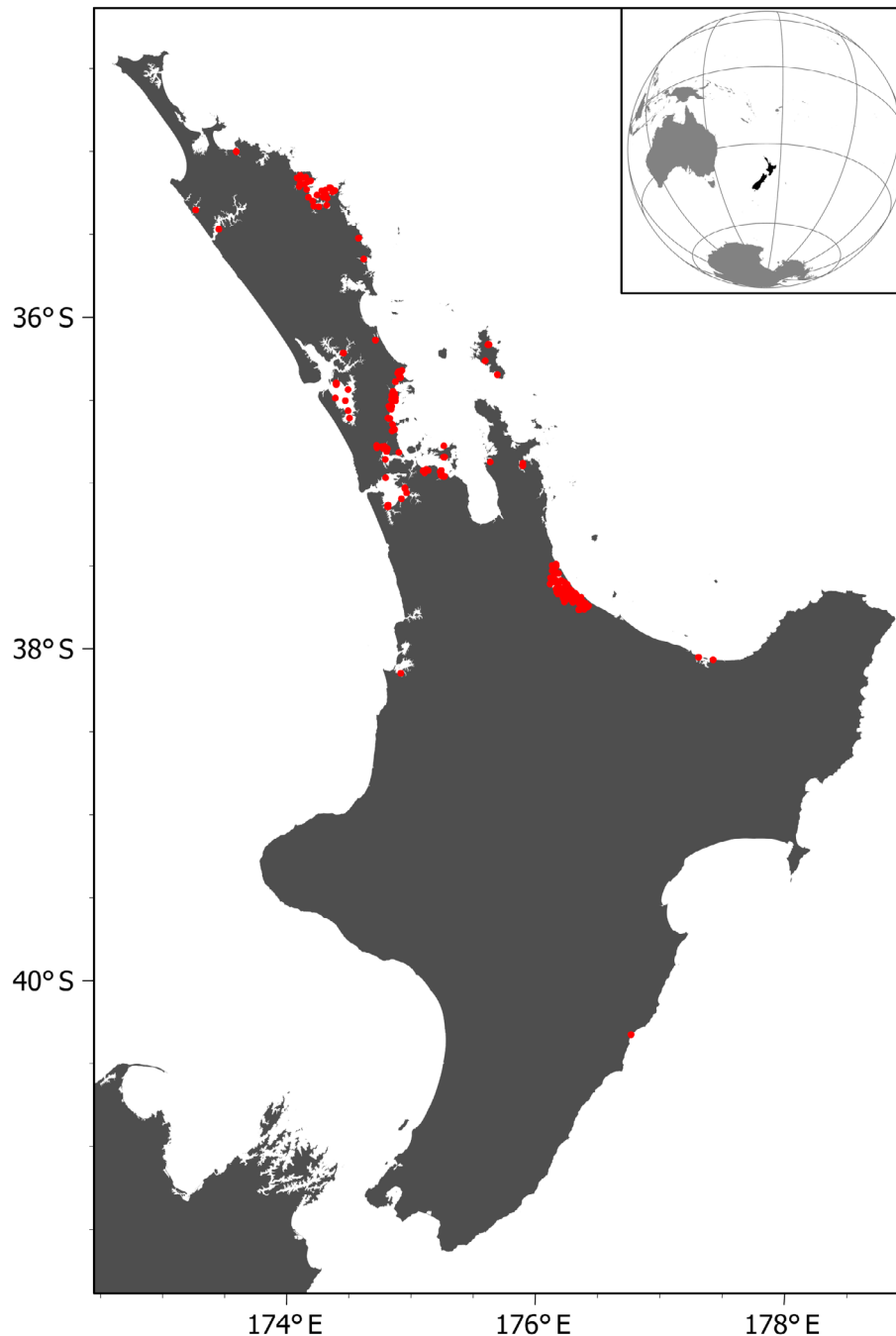


FIGURE 1 Sampling locations (red dots) in northern North Island of New Zealand.

shell fractions rather than median grain size to characterize sediment type, allowing more detailed analysis of the influence of sediment structure on ecosystem interactions (de Juan et al., 2013). Sediment organic matter content (Org, %) was quantified as loss on ignition (400°C for 5.5 h) after drying to a constant weight (60°C) (Mook & Hoskin, 1982). The microphytobenthic biomass of the sediments (i.e., chlorophyll *a* content [chl *a*], in micrograms per gram) was quantified by extracting chlorophyll *a* from freeze-dried sediments by boiling in 95% ethanol, then

analyzing the extract on a spectrophotometer (UV1800; Shimadzu, Kyoto, Japan) (Sartory, 1982).

Only samples collected during summer (October–February) were included and sites within estuaries were at least 50 m apart (to ensure our assumption of independence among samples for the analysis—see next section). At each site, a variable number of replicate cores were used to sample the macrofaunal community (ranging from 3 to 12 replicate cores depending on the study/monitoring dataset) (Hewitt et al., 2021). To ensure

macrofaunal community data were comparable between sites (and datasets), three replicate cores were averaged, resulting in a single estimate of macrofaunal community data for each site (which was paired to a single measure of environmental data). For studies with more than three replicate cores (i.e., 6–12), three cores were randomly selected without replacement and averaged to create a single macrofaunal community data for that site. The dataset was further trimmed to exclude samples where both *Macomona* and *Austrovenus* were absent. The final dataset used in the analysis consisted of paired environmental and macrofaunal data from 580 samples (unique sites) across 29 estuaries.

The final dataset was split into three categories according to the level of sediment mud content: low (<12%), moderate (12%–25%), and high (>25%). These sediment mud content values were based on results from previous research in northern New Zealand estuaries, for example, Stephenson et al. (2022) (12%), Rodil et al. (2013) (10% and 20%), Thrush et al. (2012) (20%) and Robertson et al. (2015) (>25%). Both *Austrovenus* and *Macomona* were present at sites ranging from very low to very high mud content, with *Macomona* occurring at sites with between 0% and 80% mud and *Austrovenus* between 0% and 87% mud (Table 1).

Structural equation modeling

Structural equation modeling is a form of path analysis where variables can be both predictors and responses enabling researchers to resolve complex ecological relationships and model interaction networks (Grace et al., 2010). Paths between variables represent hypothesized causal relationships (based on preexisting knowledge or theory) and SEM tests the null hypothesis that the supposed causal structure is true for the data. The null hypothesis is accepted if $p > 0.05$, and a higher p value gives stronger evidence that the structure is appropriate. An advantage of SEMs is that they can be depicted graphically, enabling visualization of indirect effects, feedbacks, and interactions between system components that may go undetected with other analytical techniques (Grace et al., 2012). Feedback loops are cyclical connections in systems that allow for indirect relationships and can have amplifying effects between components impacting future conditions (Kéfi et al., 2016). They may be common in natural systems and have strong effects on overall ecosystem structure; therefore, the ability to analyze these is extremely valuable when studying ecosystem change. Analyses that allow for cyclic and indirect connections are more powerful than analyzing simple covariance because the effects of other

TABLE 1 Bivalve abundance, abundance conditional on presence, and occurrence in low (0%–12%), moderate (12%–25%), and high (>25%) mud content datasets (n core⁻¹).

Bivalve and life stage	Abundance conditional on		
	Abundance	presence	Occurrence
Low			
Aus juv	4 ± 0.7 (1)	6 ± 0.9 (2)	208 (75)
Aus ad	6 ± 0.6 (2)	6 ± 0.5 (3)	220 (79)
Mac juv	2 ± 0.2 (0)	3 ± 0.3 (1)	163 (59)
Mac ad	2 ± 0.1 (1)	2 ± 0.1 (2)	205 (74)
Moderate			
Aus juv	2 ± 0.3 (1)	4 ± 0.4 (1)	123 (64)
Aus ad	6 ± 0.7 (2)	7 ± 0.8 (4)	161 (83)
Mac juv	1 ± 0.1 (0)	1 ± 0.1 (1)	108 (56)
Mac ad	2 ± 0.2 (2)	3 ± 0.2 (2)	153 (79)
High			
Aus juv	1 ± 0.2 (0)	2 ± 0.4 (1)	92 (58)
Aus ad	5 ± 0.6 (1)	6 ± 0.7 (3)	117 (73)
Mac juv	1 ± 0.1 (0)	1 ± 0.1 (1)	89 (56)
Mac ad	2 ± 0.2 (2)	3 ± 0.1 (3)	118 (74)

Note: Abundance values are mean ± SE and median (in parentheses). Occurrence values indicate the number of samples and percentage of samples (in parentheses) with individuals present. “Abundance conditional on presence” presents the mean and median abundances from only samples where the species was present.

Abbreviations: Aus ad, *Austrovenus* adult abundance; Aus juv, *Austrovenus* juvenile abundance; Mac ad, *Macomona* adult abundance; Mac juv, *Macomona* juvenile abundance.

variables on each relationship and asymmetric relationships are accounted for. This means that the true effects of one variable on another can be more clearly defined in the context of the wider ecosystem. In this study, SEMs were used to assess the complex interrelationships between environmental factors, and adults and juveniles of the two key benthic bivalve species *Austrovenus* and *Macomona*. Changes in ecosystem interactions with increasing ecosystem stress (sediment mud content) were assessed by comparing model structure and relationships across datasets with different mud content ranges.

Firstly, a conceptual model was constructed based on known relationships from the literature and included all plausible relationships between variables (Figure 2, Table 2). Prior to modeling, data were centered and standardized (by subtracting the mean and dividing by the standard deviation, for each variable) so that all variables had a mean of zero and a standard deviation of one (Clarke et al., 2014). For each dataset, the conceptual model was used as the initial model, which was then modified and optimized by removing nonsignificant paths to produce a final

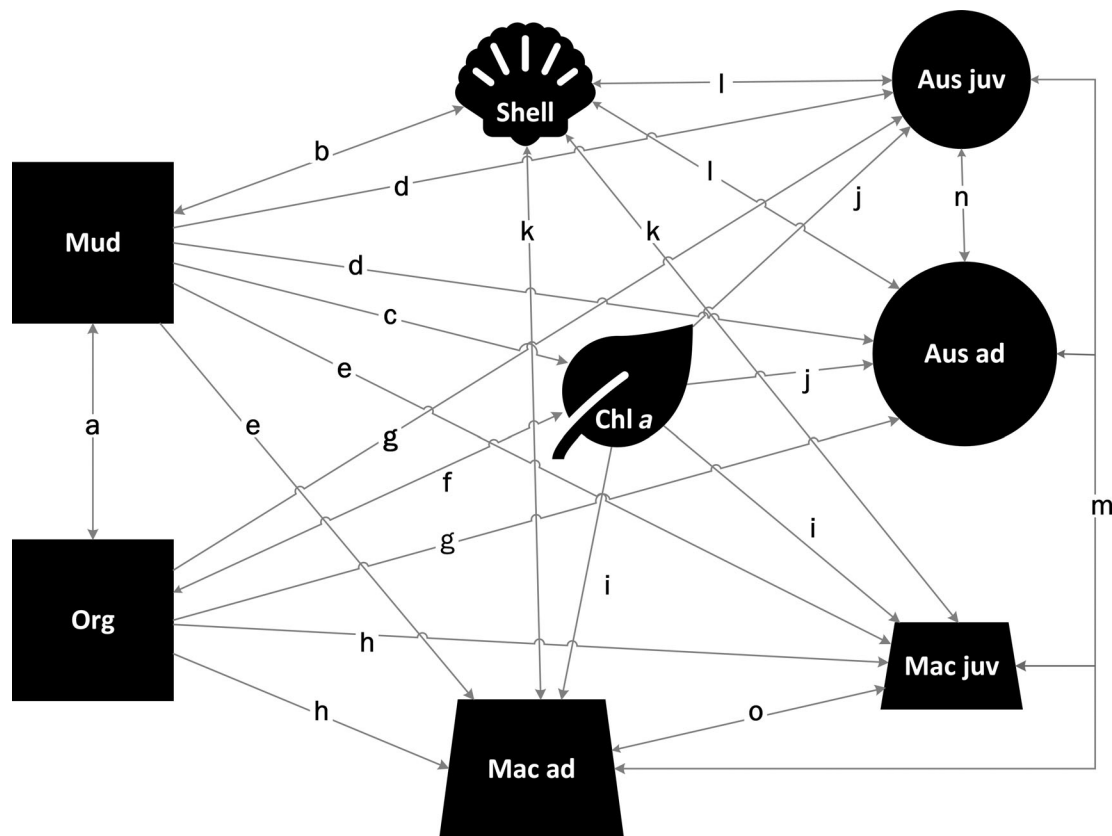


FIGURE 2 Conceptual base model indicating potential interactions between network components based on known relationships from the literature (labeled a–o; Table 2). Aus ad, *Austrovenus* adult abundance; Aus juv, *Austrovenus* juvenile abundance; chl *a*, microphytobenthic biomass; Mac ad, *Macomona* adult abundance; Mac juv, *Macomona* juvenile abundance; Mud, sediment mud content; Org, sediment organic matter content; Shell, sediment shell content.

model with adequate fit (Grace et al., 2010). The overall model fit was the most important statistic, and nonsignificant paths were not always dropped if they were important for the overall model fit. Model fit was assessed using the chi-square (χ^2) test statistic with $p > 0.05$ indicating acceptable model fit. SEMs were built using MPlus 8 (Muthen & Muthen, 2017) (see Appendix S1: Table S2 for code). For none of the datasets were all the conceptual paths able to be retained in the model, and none of the datasets gave good fits for the models of the other datasets.

RESULTS

The interaction networks representing low (<12%), moderate (12%–25%), and high (>25%) mud content sediments showed changes in interaction strength and connections congruent with changing sedimentary environment and increasing stressor levels (Figure 3). There were similarities in overall model structure but distinct differences; models of low and high mud content ecosystems had simpler interaction network architecture,

compared with the moderate mud content model, which had more paths yet fewer feedback loops (Table 3, Figure 3). In addition, there were stronger relationships in models of low mud content (mean coefficient 0.78; Table 3) compared with models with moderate and high mud content (mean coefficient 0.22 and 0.32 respectively; Table 3).

The influence of mud on other model components increased from low to high models, specifically negative effects on *Austrovenus* and *Macomona* were observed. At low levels (<12%) sediment mud content had no direct effects on either bivalve species, but as stress increased, at moderate levels (12%–25%), there were direct negative effects on the juveniles of both species. Mud content had a positive effect on *Austrovenus* adults in the moderate mud content model; mean densities of adult *Austrovenus* were higher than juveniles in moderate and high mud conditions, whereas densities were similar in low mud (Table 1). At high levels (>25%) mud had direct negative effects on *Austrovenus* juveniles and *Macomona* adults, and *Macomona* juveniles were indirectly negatively affected through a negative impact of mud on chl *a*.

TABLE 2 Interaction network relationships from the literature corresponding to path diagram Figure 2.

Path	Variable 1	Variable 2	Relationship	Source
a	Sediment mud content	Organic matter content	Co-occurrence of higher organic matter content with fine particles.	Huettel and Rusch (2000), Thrush et al. (2008), Pratt et al. (2013)
b	Sediment mud content	Sediment shell content	Coarse sediments and sediment mud content are generally negatively correlated.	Thrush et al. (2008)
c	Sediment mud content	Chlorophyll <i>a</i>	Muddy sediments tend to have higher microphytobenthos biomass, but high levels of fine sediments can have a negative effect on microphytobenthos biomass.	Cahoon et al. (1999), van de Koppel et al. (2001), Pratt et al. (2014)
d	Sediment mud content	<i>Austrovenus</i>	Fine sediments negatively impact abundance of <i>Austrovenus</i> by clogging gills and filter-feeding structures and by burying/smothering small juveniles.	Thrush et al. (2003, 2004), Cummings et al. (2009), Pratt et al. (2013)
e	Sediment mud content	<i>Macomona</i>	Fine sediments negatively impact abundance of <i>Macomona</i> through reduction in burial of post-settlement juveniles.	Thrush et al. (2003, 2004), Cummings et al. (2009), Pratt et al. (2013)
f	Organic matter content	Chlorophyll <i>a</i>	Sediment organic matter content and Chlorophyll <i>a</i> are positively correlated. Microphytobenthos (and degraded microphytobenthos) is part of the sediment organic matter pool.	Miller et al. (1996), Ehrenhauss et al. (2004), Pratt et al. (2013)
g	Organic matter content	<i>Austrovenus</i>	Like all animals, <i>Austrovenus</i> must consume organic matter to derive energy and essential compounds. Although a suspension feeder, part of <i>Austrovenus</i> ' diet is comprised of resuspended sediment organic matter.	
h	Organic matter content	<i>Macomona</i>	As a surface deposit feeder, sediment organic matter content provides a food source for <i>Macomona</i> .	Rhoads and Boyer (1982), Pridmore et al. (1990), Thrush et al. (2006), Lohrer et al. (2016)
i	Chlorophyll <i>a</i>	<i>Macomona</i>	Microphytobenthos provide a food source for <i>Macomona</i> and have a positive effect on abundance.	Lelieveld et al. (2004), Thrush et al. (2006), Van Colen et al. (2013, 2014), Pratt et al. (2014, 2015), Harris et al. (2015)
j	Chlorophyll <i>a</i>	<i>Austrovenus</i>	Resuspended microphytobenthos provide a food source for <i>Austrovenus</i> and have a positive effect on abundance. <i>Austrovenus</i> strongly influence microphytobenthos productivity through bioturbation, pore water nutrient release, and ammonium excretion.	Lelieveld et al. (2004), Thrush et al. (2006), Sandwell et al. (2009), Van Colen et al. (2013, 2014), Pratt et al. (2014, 2015), Harris et al. (2015)
k	Sediment shell content	<i>Macomona</i>	Coarse fraction sediment especially shell material enhances settlement of <i>Macomona</i> . <i>Macomona</i> may contribute a small amount of shell material.	

(Continues)

TABLE 2 (Continued)

Path	Variable 1	Variable 2	Relationship	Source
l	Sediment shell content	<i>Austrovenus</i>	<i>Austrovenus</i> density is highest in coarse sediments. Coarse fraction sediment especially shell material enhances settlement <i>Austrovenus</i> . <i>Austrovenus</i> contribute shell material.	Thrush et al. (2008), Smith et al. (2010)
m	<i>Austrovenus</i>	<i>Macomona</i>	The density of each of these species can influence the abundance of the other. High densities of adults have been shown to result in high rates of consumption and disruption of settling larvae. High densities of <i>Austrovenus</i> can reduce the abundance of <i>Macomona</i> especially post-settlement individuals. Other studies have shown positive correlation between adults of these species. Negative interactions between adult <i>Macomona</i> and juvenile <i>Austrovenus</i> have also been found.	Brenchley (1981, 1982), Volkenborn et al. (2009), Woodin and Jackson (1979), Thrush, Hewitt, et al. (1996), Thrush et al. (1997, 2006), Whitlatch et al. (1997), Pratt et al. (2014), Van Colen et al. (2014), Stephenson et al. (2022)
n	<i>Austrovenus</i> juvenile	<i>Austrovenus</i> adult	Positive population feedbacks. Adults can affect the density of juvenile conspecifics.	Thrush, Hewitt, et al. (1996)
o	<i>Macomona</i> juvenile	<i>Macomona</i> adult	Positive population feedbacks. Higher densities of adult <i>Macomona</i> can positively or negatively affect juvenile conspecifics, and this effect can be context specific (dependent on sediment type).	Thrush et al. (1992, 1997), Hewitt et al. (1996), Thrush, Hewitt, et al. (1996)

Mud content had a positive effect on chl *a* in the low mud model, no direct effect in the moderate model, and the relationship switched to negative (although insignificant) in the high mud model. This mud–chl *a* relationship is likely to have indirect effects on other components and interactions in the ecosystem, in particular the positive effects of chl *a* on bivalve abundances, which were absent in the high mud model. There was a consistent positive effect of organic matter content on chl *a*, which had an increasing effect from low to high mud content.

A grazer–food source interaction was indicated by a feedback between chl *a* and *Macomona* adults, and a positive effect of chl *a* on *Macomona* juveniles in the low mud model. Microphytobenthic biomass increased with increasing mud content (Table 4), and in the moderate model the positive effect of chl *a* on *Macomona* adults remained (a food source) but the link indicating a negative effect of grazing on chl *a* disappeared. Furthermore, the positive effect of chl *a* on *Macomona* juveniles was absent in moderate mud model. There was no evidence for *Macomona* grazing interaction in high mud, but

there was a feedback loop where *Macomona* juveniles facilitated microphytobenthos, while microphytobenthos inhibited *Macomona* juveniles (Appendix S1: Table S3).

Intraspecific adult–juvenile interactions were consistent across all mud conditions for both species, although the magnitude of these relationships changed (Figure 3). *Macomona* adults consistently had a positive effect on juveniles, a relationship that strengthened with increasing stress (Appendix S1: Table S3). For *Austrovenus*, increasing numbers of juveniles led to increasing densities of adults at the temporal and spatial scales of the models, but this relationship weakened above 12% mud content as increasing mud negatively affected the number of juveniles (Appendix S1: Table S3).

In the low mud model, there was a strong cyclical feedback between *Austrovenus* adults, juveniles, and shell content; shell content negatively affected both *Austrovenus* juveniles and adults, juveniles positively affected adults, and adults had a positive effect on sediment shell content. The net effect of this was an overall positive feedback loop (sum of path coefficients = +2.3; Appendix S1: Table S3), stabilized to some degree by shell

content. In moderate levels of mud, this loop did not occur as there was no link between shell and *Austrovenus* juveniles. Under high mud conditions, there was a feedback loop only involving positive paths (Appendix S1: Table S3), that is, *Austrovenus* adults enhanced shell, shell

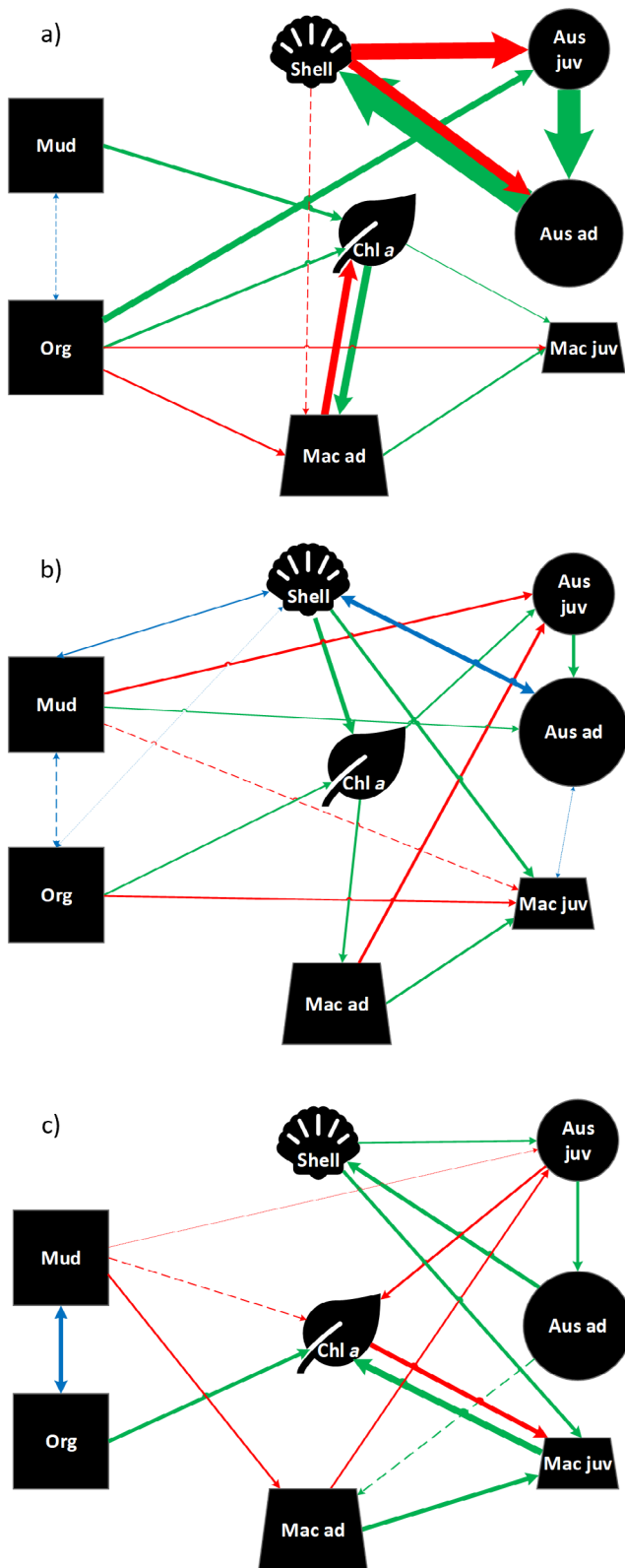


TABLE 3 Summary statistics for structural equation models fitted with data categorized by levels of low (0%–12%), moderate (12%–25%), and high (>25%) mud content.

Measure	Low	Moderate	High
Mud content	<12%	12%–25%	>25%
No. samples	278	192	160
No. significant paths	11	13	12
No. insignificant paths	4	4	3
Total no. paths	15	17	15
No. negative paths	6	4	6
No. positive paths	8	8	8
Covariances	1	5	1
χ^2 test of model fit	10.2	8.15	8.69
Model fit <i>p</i> value	0.7	0.7	0.8

enhanced *Austrovenus* juveniles, and juveniles enhanced *Austrovenus* adults; shell content is required to maintain *Austrovenus* populations. So, as mud increases, the negative effect of shell on *Austrovenus* juveniles initially disappears (moderate mud model) and then becomes positive (high mud model).

Direct interspecific interactions between *Macomona* and *Austrovenus* were absent in low mud ecosystems (no direct links in the low mud model), but above 12% mud *Macomona* adults had a negative effect on juvenile *Austrovenus*. This relationship remained in high mud where *Austrovenus* adults had a weak positive effect on *Macomona* adults creating an interspecies loop indicating that interactions between the two species were developing as stress increases. Although *Macomona* did not appear to contribute to the shell content of the sediments, the Shell–*Austrovenus* loop influenced *Macomona*. In low mud, shell content had a negative impact on adult *Macomona* (albeit weak and insignificant), and in moderate and high mud conditions, there was a positive effect of shell content on juvenile *Macomona*. Like *Austrovenus*, shell appears to act as a facilitator in the harsher mud conditions.

FIGURE 3 Ecosystem interaction networks in (a) low (<12%), (b) moderate (12%–25%), and (c) high (>25%) mud content sediments. Green arrows indicate positive effects, red arrows indicate negative effects, and blue double-headed arrows indicate covariance. Line thickness scales with path coefficient indicating effect size and dotted lines indicate insignificant ($p > 0.1$) paths that were retained for model significance. For actual path coefficients and significance values see Appendix S1: Table S3. Aus ad, *Austrovenus* adult abundance; Aus juv, *Austrovenus* juvenile abundance; chl a, microphytobenthic biomass; Mac ad, *Macomona* adult abundance; Mac juv, *Macomona* juvenile abundance; Mud, sediment mud content; Org, sediment organic matter content; Shell, sediment shell content.

TABLE 4 Summary statistics for variables in low (0%–12%), moderate (12%–25%), and high (>25%) mud content datasets.

Variable	Units	Mean	Median	Min	Max	SD
Low						
Shell	%	7.6	2.2	0	66	12
Mud	%	4.9	4.0	0	12	3.7
Org	%	1.5	1.3	0.4	7.6	0.9
Chl <i>a</i>	µg g ⁻¹	8.1	6.8	0.2	28	5.4
Species	no. core ⁻¹	14	14	1	26	4
Moderate						
Shell	%	7.2	3.3	0	80	11
Mud	%	18	18	12	25	3.6
Org	%	2.2	1.8	0.8	7.1	1.0
Chl <i>a</i>	µg g ⁻¹	14	12	2.7	49	7.5
Species	no. core ⁻¹	14	14	2	25	4
High						
Shell	%	6.7	1.7	0	48	11
Mud	%	40	35	25	88	14
Org	%	3.2	2.7	1.2	8.1	1.4
Chl <i>a</i>	µg g ⁻¹	17	16	1.1	46	8.4
Species	no. core ⁻¹	13	13	3	20	4

Abbreviations: chl *a*, microphytobenthic biomass; Max, maximum; Min, minimum; Mud, sediment mud content; Org, sediment organic matter content; Shell, sediment shell content; Species, total taxa.

DISCUSSION

The main aim of this study was to determine how sedimentary environment, particularly increasing sediment mud content, can influence species–environment interactions and intra- and interspecific interactions of two key bivalve species. We investigated potential mechanisms driving interactions between these species and their environment in different sedimentary conditions. The increase in number of paths from the low to the moderate mud model was counter to our original prediction of simpler system architecture with increasing stress. That this occurs in conjunction with a decrease in the mean coefficients may be indicative of increasing variability in relationships occurring with increasing environmental stress. Increasing or changing variance can be an indicator of an ecosystem approaching a threshold or tipping point (Hewitt & Thrush, 2009; Kéfi et al., 2014; Scheffer et al., 2009), and other studies have indicated thresholds in ecosystem function at 12% (Stephenson et al., 2022) and 19.9% mud content (Thrush et al., 2012). Therefore, our moderate (12%–25%) mud content model may be encompassing or representing a transition point in ecosystem dynamics where interaction networks break down

and shift to an alternate state. The change in role and scale of influence of mud content as a factor in each model is a clear example of this, as mud content increases, so does its influence on the interaction network. In the low mud model, mud only directly affects one other component (chl *a*), a positive relationship indicating a positive effect of limited amounts of mud on food resources for both bivalves (Figure 3a). In the moderate and high mud models, mud directly affects three other components (Figure 3b,c).

Understanding ecosystem resilience to stress

Organism size is a critical factor in ecosystem functioning (Norkko et al., 2013; Thrush et al., 2006; Thrush & Dayton, 2002), and the size distribution of a population profoundly influences overall community structure and population persistence (Lawton et al., 1990; Petchey et al., 2008). Different life stages may be disproportionately affected by different types of stressors such as heat wave events or increasing predation pressure (McGreer, 1982; Sorte et al., 2010). Our interaction networks show that occurrence of negative effects on population cohorts (e.g., juveniles) will have significant flow-on effects for the rest of the system, and that effects may be worse in already stressed systems. These models give a mechanistic understanding of how added stress and/or population structure changes may affect ecosystem interactions in different environments. They may also help with understanding how populations in ecosystems with different levels of sedimentation stress may recover following disturbance or die-off. For example, growth rates and maximum sizes of bivalves may be reduced in environments with higher levels of existing stressors such as sediment mud content. If bivalves take longer to reach maturity, the positive effects of important feedback loops may also be reduced.

Studying feedback loops in SEMs can help us understand how population maintenance of species can be different in different environmental settings, or as stress increases. Here we show that positive species–environment feedbacks can occur at high levels of stress, which may indicate adaptation, environmental plasticity, and resilience. Occurrence of antagonistic interspecific interactions as environmental stress increases has implications for population maintenance and overall community structure. Interactions that reduce the settlement or feeding of another species may eventually result in loss of a species from an ecosystem, although the effect may happen over relatively large time-scales (Bengtsson, 1989; Ejdung & Elmgren, 1998). Testing scenarios with interaction networks using real or hypothetical data may provide progress for mitigation strategies or

restoration efforts. For example, these types of models could be coupled with monitoring programs that include analysis of species life stage or size frequency and may enable early detection or markers of population decline.

Abundances and occurrence of *Macomona* and *Austrovenus* varied among the three datasets (Table 1), which potentially influenced our model results, as relationships may be more stable where abundances are higher. A caveat of using SEMs to interpret ecological systems is that relationships between variables can only be modeled as linear, when in reality, nonlinear relationships are more likely. By categorizing the datasets into three levels of mud content, we limit the impacts of potential nonlinearities in relationships between sediment mud content and other variables. The “high mud” lower limit (>25%) is not very high relative to stressed ecosystems subject to high sedimentation rates. The mud content range for this group is wide, 25%–88% (mean = 40%, median = 35%), and 25% mud is higher than mud content thresholds identified in other studies (Douglas et al., 2019; Thrush et al., 2012). Given the breadth of ecosystems covered by the high mud model, it may be surprising that this model has the best fit, despite the lowest sample size. This may indicate that beyond 25% mud content systems have shifted to an alternate stable state with different interaction network structures, characterized by changes in intra- and inter-specific interactions.

Ecosystem interactions

There are two standout features consistent in the low and high mud models: (1) a feedback loop involving *Austrovenus* (both adults and juveniles) and sediment shell content, and (2) a grazer interaction loop between *Macomona* (both adults and juveniles) and chl *a*. These loops show different characteristics in the high and low mud content ecosystems, but only remnants of these loops are present in the moderate model, which may be another indication of a community or ecosystem in a state of reorganization. This may provide an example of ecosystem bistability, where there are two alternate stable states (van der Heide et al., 2011), in this case, low and high mud, separated by a transitional state, moderate mud.

The positive feedback loop between adult and juvenile *Austrovenus* with shell content may be indicative of self-engineering of a favorable environment by this species occurring in high stress conditions. Other studies have shown increasing importance of the effects of ecosystem engineering shellfish with increasing stress (e.g., Donadi et al., 2013); however, such studies do not

usually account for feedbacks. In low mud areas, shell has a negative effect on juveniles, probably through interference with mobility (although the overall net effect of the Shell–juvenile–adult loop is positive). In the moderate mud areas, there is no effect of shell on juvenile *Austrovenus*, but a positive covariance between adults and shell indicates that this link is important under a broad range of sedimentary conditions. The persistence of this loop, although with slight changes in structure, may reflect *Austrovenus*' resilience to changing sedimentary conditions and the environmental plasticity of the species. Although the positive adult–juvenile interaction for *Austrovenus* is not completely clear here, there is corroborating evidence from Europe of enhancement of juveniles by adult venerids through ecosystem engineering and sediment stabilization (Donadi et al., 2014).

The change in the *Macomona* grazer interaction loop from low to high models indicates that as sedimentation stress increases, food availability may be a less important driver of *Macomona* abundance since microphytobenthic biomass is greatest in high mud conditions. Environmental conditions or other external factors such as antagonistic interactions with species not included here may be more important. For example, *Macomona* are not strict deposit feeders and may switch to suspension feeding depending on the environmental setting (Pridmore et al., 1991). Sediment type, especially shell content, is known to influence bivalve behavior, predation rates, and recruitment processes such as larval settlement and movement of post-larval bivalves (Cummings et al., 2009; Thrush, Hewitt, et al., 1996). The increasing positive effect of shell content on juvenile *Macomona* in our study suggests that as mud content increases, larger shell particles may become more important for recruitment or settlement processes, and the high mud model shows that *Austrovenus* indirectly facilitates *Macomona* through increasing sediment shell content.

In all our models, *Macomona* adults consistently positively influenced juvenile *Macomona* and this effect becomes more important with increasing mud content. Adult *Macomona* can facilitate colonization of juvenile conspecifics (Thrush et al., 1992); however, this effect is known to be density dependent (Thrush, Hewitt, et al., 1996). *Macomona* can undergo post-larval movement or secondary settlement to different areas of the shore (Cummings et al., 1993; Petuha et al., 2006; Roper et al., 1992b) and this may influence the abundance of different size classes, the adult–juvenile interactions, and the spatial distribution of this species. Adults of a similar species, *Macoma balthica*, can reduce the growth of juveniles; a context-specific effect is evident only in a muddy-sand habitat but not a sandy habitat (Ólafsson, 1989). *Macomona* adult–juvenile interactions have similarly been shown to differ with sediment

types, with highest juvenile densities associated with higher adult densities at muddy sites (Thrush, Hewitt, et al., 1996). This corroborates our results showing a stronger positive interaction under higher levels of stress (mud).

There is a consistent positive effect of sediment organic matter content on chlorophyll *a*. Growth of microphytobenthos is known to be supported by nutrients from the breakdown of organic matter in the sediments (Lohrer et al., 2015; Lohrer, Thrush, & Gibbs, 2004; Sundback et al., 2003; Sundback & Miles, 2002); in our models, this effect increases as sediment mud content (and organic matter content) increases. Chlorophyll *a* is indicative of system productivity and also provides a food source for both filter-feeding *Austrovenus* and deposit-feeding *Macomona*. Chlorophyll *a* is central to models as microphytobenthic biomass is directly linked to the abiotic conditions (e.g., supply of nutrients from pore water and organic matter breakdown, sediment size determines the surface area available to colonize), and connected to the abundance of both bivalve species.

Austrovenus and *Macomona* both exist and co-occur, across a range of sedimentary environments (0%–80% mud content) in New Zealand estuaries, and both are negatively affected by the increasing sediment mud content. It is not surprising then that interactions among conspecifics and between these species change across the sedimentary gradient (0%–87% mud content) studied here. Stephenson et al. (2022) found asymmetrical interactions but only using adult data. Here, we build on this by including juvenile data and show how this changes across the sedimentary gradient. The emergence of interspecific interactions only at higher levels of stress (i.e., outside the optimum sediment type for the species) may reflect greater pressures on species due to lowered environmental suitability or changes in behavior in different sedimentary environments (Pridmore et al., 1991). For example, the antagonistic effect of *Macomona* adults on *Austrovenus* juveniles in moderate and high mud (i.e., beyond the 11% mud optimum for *Austrovenus*) may be caused by a combination of changes in sedimentary conditions and *Macomona* feeding activities that result in reduced *Austrovenus* larval settlement (Lelieveld et al., 2004; Thrush, Pridmore, & Hewitt, 1996). Similarly, *Austrovenus* juveniles negatively impact chl *a* and possibly have a negative indirect effect on *Macomona* juveniles, but only in high mud. Surface bioturbation activities of *Austrovenus* can disrupt microphytobenthos and its interaction with *Macomona* (Van Colen et al., 2014), and our results suggest this disruption is context dependent and may be because muddy environments have finer surface sediments (which tend to have higher chl *a* stock) that are more easily moved and resuspended by *Austrovenus* activity. Interactions between adults of the two species are only evident in high mud

conditions where there is a weak positive effect of *Austrovenus* on *Macomona*. Other studies have found positive correlation between adults of these species suggesting facilitation (Pratt et al., 2013); however unlike our study, this relationship has been shown to be lost with increasing stress (Van Colen et al., 2014).

These interaction networks only include one key stressor, so they cannot be used to evaluate multiple stressor effects, but they may provide a useful starting point for hypothesizing the negative impacts of another stressor on interactions in different systems. Our analyses show that changes in environmental conditions, particularly increasing stress, can alter species' life stage interactions, interactions between species, and interactions between species and their environment. Using the space-for-time substitution provides a means to estimate future ecosystem change, accompanying changes in terrigenous sediment loading to the marine environment. If indeed there are alternate ecosystem networks related to mud content, this has huge implications for management decisions and ecosystem restoration interventions.

ACKNOWLEDGMENTS

We gratefully acknowledge the use of the data collected from multiple studies, especially: Casper Kraan (Marie-Curie International Outgoing Fellowship 298380); Simon Thrush (Marsden fund of the Royal Society of New Zealand NIW1102); the National Institute of Water and Atmospheric Research NZ (NIWA) Hamilton's many past and present Marine Ecology team members and SSIF funding over the years; Land Information New Zealand for funding the Bay of Islands data collection; and Tarn Drylie and the Auckland Council for their marine monitoring. We thank Grady Petersen for designing Figure 1. The analysis and writing of this manuscript were funded by NIWA's Coast and Oceans SSIF funding (projects COME2101 and COME2201).

CONFLICT OF INTEREST

The authors declare no conflict of interest.


DATA AVAILABILITY STATEMENT

No data were collected for this study. The data used in the analysis of this study came from previous studies that are cited in Appendix S1: Table S1.

ORCID

Emily J. Douglas  <https://orcid.org/0000-0002-9728-6943>

Judi Hewitt  <https://orcid.org/0000-0002-5083-9715>

Andrew M. Lohrer  <https://orcid.org/0000-0002-3893-6539>

Fabrice Stephenson  <https://orcid.org/0000-0002-9500-5204>

REFERENCES

- Anderson, M. J. 2008. "Animal-Sediment Relationships Revisited: Characterising Species' Distributions along an Environmental Gradient Using Canonical Analysis and Quantile Regression Splines." *Journal of Experimental Marine Biology and Ecology* 366: 16–27.
- Armsworthy, S. L., B. A. MacDonald, and J. E. Ward. 2001. "Feeding Activity, Absorption Efficiency and Suspension Feeding Processes in the Ascidian, *Halocynthia pyriformis* (Stolidobranchia: Ascidiacea): Responses to Variations in Diet Quantity and Quality." *Journal of Experimental Marine Biology and Ecology* 260: 41–69.
- Bell, J. J., E. McGrath, A. Biggerstaff, T. Bates, H. Bennett, J. Marlow, and M. Shaffer. 2015. "Sediment Impacts on Marine Sponges." *Marine Pollution Bulletin* 94: 5–13.
- Bengtsson, J. 1989. "Interspecific Competition Increases Local Extinction Rate in a Metapopulation System." *Nature* 340: 713–5.
- Bishop, M. J., and C. H. Peterson. 2006. "Direct Effects of Physical Stress Can be Counteracted by Indirect Benefits: Oyster Growth on a Tidal Elevation Gradient." *Oecologia* 147: 426–33.
- Blois, J. L., J. W. Williams, M. C. Fitzpatrick, S. T. Jackson, and S. Ferrier. 2013. "Space Can Substitute for Time in Predicting Climate-Change Effects on Biodiversity." *Proceedings of the National Academy of Sciences* 110: 9374–9.
- Brenchley, G. 1982. "Mechanisms of Spatial Competition in Marine Soft-Bottom Communities." *Journal of Experimental Marine Biology and Ecology* 60: 17–33.
- Brenchley, G. A. 1981. "Disturbance and Community Structure: An Experimental Study of Bioturbation in Marine Softbottom Environments." *Journal of Marine Research* 39: 767790.
- Bulmer, R. H., F. Stephenson, D. Lohrer, C. Lundquist, A. Madarasz-Smith, C. Pilditch, S. Thrush, and J. Hewitt. 2022. "Informing the Management of Multiple Stressors on Estuarine Ecosystems Using an Expert-Based Bayesian Network Model." *Journal of Environmental Management* 301: 113576.
- Cahoon, L. B., J. E. Nearhoof, and C. L. Tilton. 1999. "Sediment Grain Size Effect on Benthic Microalgal Biomass in Shallow Aquatic Ecosystems." *Estuaries* 22: 735–41.
- Capmourteres, V., and M. Anand. 2016. "Assessing Ecological Integrity: A Multi-Scale Structural and Functional Approach Using Structural Equation Modeling." *Ecological Indicators* 71: 258–69.
- Clarke, K. R., R. N. Gorley, P. J. Somerfield, and R. M. Warwick. 2014. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 3rd ed. Plymouth: PRIMER-E.
- Cummings, V., K. Vopel, and S. Thrush. 2009. "Terrigenous Deposits in Coastal Marine Habitats: Influences on Sediment Geochemistry and Behaviour of Post-Settlement Bivalves." *Marine Ecology Progress Series* 383: 173–85.
- Cummings, V. J., R. D. Pridmore, S. F. Thrush, and J. E. Hewitt. 1993. "Emergence and Floating Behaviours of Post-Settlement Juveniles of *Macomona liliana* (Bivalvia: Tellinacea)." *Marine Behaviour and Physiology* 24: 25–32.
- Cummings, V. J., R. D. Pridmore, S. F. Thrush, and J. E. Hewitt. 1995. "Post-Settlement Movement by Intertidal Benthic Macroinvertebrates: Do Common New Zealand Species Drift in the Water Column?" *New Zealand Journal of Marine and Freshwater Research* 29: 59–67.
- de Juan, S., S. F. Thrush, and J. E. Hewitt. 2013. "Counting on β -Diversity to Safeguard the Resilience of Estuaries." *PLoS One* 8: e65575.
- de Roos, A. M. 2021. "Dynamic Population Stage Structure Due to Juvenile–Adult Asymmetry Stabilizes Complex Ecological Communities." *Proceedings of the National Academy of Sciences* 118: e2023709118.
- Donadi, S., E. M. van der Zee, T. van der Heide, E. J. Weerman, T. Piersma, J. van de Koppel, H. Olf, M. Bartelds, I. van Gerwen, and B. K. Eriksson. 2014. "The Bivalve Loop: Intra-Specific Facilitation in Burrowing Cockles through Habitat Modification." *Journal of Experimental Marine Biology and Ecology* 461: 44–52.
- Donadi, S., J. Westra, E. J. Weerman, T. van der Heide, E. M. van der Zee, J. van de Koppel, H. Olf, T. Piersma, H. W. van der Veer, and B. K. Eriksson. 2013. "Non-trophic Interactions Control Benthic Producers on Intertidal Flats." *Ecosystems* 16: 1325–35.
- Douglas, E. J., A. M. Lohrer, and C. A. Pilditch. 2019. "Biodiversity Breakpoints along Stress Gradients in Estuaries and Associated Shifts in Ecosystem Interactions." *Scientific Reports* 9: 17567.
- Douglas, E. J., C. A. Pilditch, A. M. Lohrer, C. Savage, L. A. Schipper, and S. F. Thrush. 2018. "Sedimentary Environment Influences Ecosystem Response to Nutrient Enrichment." *Estuaries and Coasts* 41: 1994–2008.
- Ehrenhauss, S., U. Witte, F. Janssen, and M. Huettel. 2004. "Decomposition of Diatoms and Nutrient Dynamics in Permeable North Sea Sediments." *Continental Shelf Research* 24: 721–37.
- Ejdung, G., and R. Elmgren. 1998. "Predation on Newly Settled Bivalves by Deposit-Feeding Amphipods: A Baltic Sea Case Study." *Marine Ecology Progress Series* 168: 87–94.
- Ellingsen, K. E., J. E. Hewitt, and S. F. Thrush. 2007. "Rare Species, Habitat Diversity and Functional Redundancy in Marine Benthos." *Journal of Sea Research* 58: 291–301.
- Ellis, J., V. Cummings, J. Hewitt, S. Thrush, and A. Norkko. 2002. "Determining Effects of Suspended Sediment on Condition of a Suspension Feeding Bivalve (*Atrina zelandica*): Results of a Survey, a Laboratory Experiment and a Field Transplant Experiment." *Journal of Experimental Marine Biology and Ecology* 267: 147–74.
- Ellis, J., J. Hewitt, D. Clark, C. Taiapa, M. Patterson, J. Sinner, D. Hardy, and S. Thrush. 2015. "Assessing Ecological Community Health in Coastal Estuarine Systems Impacted by Multiple Stressors." *Journal of Experimental Marine Biology and Ecology* 473: 176–87.
- Gatehouse, J. 1971. "Sediment Analysis." In *Procedures in Sedimentology and Petrology*, edited by R. Carver, 59–94. New York: Wiley Interscience.
- Grace, J. B., T. M. Anderson, H. Olf, and S. M. Scheiner. 2010. "On the Specification of Structural Equation Models for Ecological Systems." *Ecological Monographs* 80: 67–87.
- Grace, J. B., D. R. Schoolmaster, G. R. Guntenespergen, A. M. Little, B. R. Mitchell, K. M. Miller, and E. W. Schweiger. 2012. "Guidelines for a Graph-Theoretic Implementation of Structural Equation Modeling." *Ecosphere* 3: art73.
- Gray, J. S. 2002. "Species Richness of Marine Soft Sediments." *Marine Ecology Progress Series* 244: 285–97.
- Harris, R., C. Pilditch, J. Hewitt, A. Lohre, C. Van Colen, M. Townsend, and S. Thrush. 2015. "Biotic Interactions

- Influence Sediment Erodibility on Wave-Exposed Sandflats.” *Marine Ecology Progress Series* 523: 15–30.
- Hawkins, A. J. S., B. L. Bayne, S. Bougrier, M. Héral, J. I. P. Iglesias, E. Navarro, R. F. M. Smith, and M. B. Urrutia. 1998. “Some General Relationships in Comparing the Feeding Physiology of Suspension-Feeding Bivalve Molluscs.” *Journal of Experimental Marine Biology and Ecology* 219: 87–103.
- Hewitt, J., R. Pridmore, S. Thrush, and V. Cummings. 1997. “Assessing the Short-Term Stability of Spatial Patterns of Macrobenthos in a Dynamic Estuarine System.” *Limnology and Oceanography* 42: 282–8.
- Hewitt, J. E., R. H. Bulmer, F. Stephenson, and S. F. Thrush. 2021. “Sampling Frequency, Duration and the Southern Oscillation Influence the Ability of Long-Term Studies to Detect Sudden Change.” *Global Change Biology* 27: 2213–24.
- Hewitt, J. E., P. Legendre, B. H. McArde, S. F. Thrush, C. Bellehumeur, and S. M. Lawrie. 1997. “Identifying Relationships between Adult and Juvenile Bivalves at Different Spatial Scales.” *Journal of Experimental Marine Biology and Ecology* 216: 77–98.
- Hewitt, J. E., and S. F. Thrush. 2009. “Do Species’ Abundances Become More Spatially Variable with Stress?” *The Open Ecology Journal* 2: 37–46.
- Hewitt, J. E., S. F. Thrush, V. J. Cummings, and R. D. Pridmore. 1996. “Matching Patterns with Processes: Predicting the Effect of Size and Mobility on the Spatial Distributions of the Bivalves *Macomona liliana* and *Austrovenus stutchburyi*.” *Marine Ecology Progress Series* 135: 57–67.
- Hohaia, A., K. Vopel, and C. A. Pilditch. 2013. “Thin Terrestrial Sediment Deposits on Intertidal Sandflats: Effects on Pore Water Solutes and Juvenile Bivalve Burial Behaviour.” *Biogeosciences Discussions* 10: 14835–60.
- Huetzel, M., and A. Rusch. 2000. “Transport and Degradation of Phytoplankton in Permeable Sediment.” *Limnology and Oceanography* 45: 534–49.
- Jacquot, M. P., K. M. Dorgan, B. Mortazavi, A. A. Kleinhuisen, and W. C. Clemo. 2018. “Macrobenthic Community Structure and Influence on Denitrification Capacity in Soft Sediments (Mobile Bay, Alabama, USA).” *Marine Ecology Progress Series* 605: 17–35.
- Kéfi, S., V. Guttal, W. A. Brock, S. R. Carpenter, A. M. Ellison, V. N. Livina, D. A. Seekell, M. Scheffer, E. H. van Nes, and V. Dakos. 2014. “Early Warning Signals of Ecological Transitions: Methods for Spatial Patterns.” *PLoS One* 9: e92097.
- Kéfi, S., M. Holmgren, and M. Scheffer. 2016. “When Can Positive Interactions Cause Alternative Stable States in Ecosystems?” *Functional Ecology* 30: 88–97.
- Lawton, J. H., M. P. Hassell, and R. M. May. 1990. “Species Richness and Population Dynamics of Animal Assemblages. Patterns in Body Size: Abundance Space.” *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 330: 283–91.
- Lelieveld, S. D., C. A. Pilditch, and M. O. Green. 2004. “Effects of Deposit-Feeding Bivalve (*Macomona liliana*) Density on Intertidal Sediment Stability.” *New Zealand Journal of Marine and Freshwater Research* 38: 115–28.
- Lohrer, A. M., S. F. Thrush, and M. M. Gibbs. 2004. “Bioturbators Enhance Ecosystem Function through Complex Biogeochemical Interactions.” *Nature* 431: 1092–5.
- Lohrer, A. M., S. F. Thrush, J. E. Hewitt, K. Berkenbusch, M. Ahrens, and V. J. Cummings. 2004. “Terrestrially Derived Sediment: Response of Marine Macrobenthic Communities to Thin Terrigenous Deposits.” *Marine Ecology Progress Series* 273: 121–38.
- Lohrer, A. M., S. F. Thrush, J. E. Hewitt, and C. Kraan. 2015. “The Up-Scaling of Ecosystem Functions in a Heterogeneous World.” *Scientific Reports* 5: 10349.
- Lohrer, A. M., S. F. Thrush, C. J. Lundquist, K. Vopel, J. E. Hewitt, and P. E. Nicholls. 2006. “Deposition of Terrigenous Sediment on Subtidal Marine Macrobenthos: Response of Two Contrasting Community Types.” *Marine Ecology Progress Series* 307: 115–25.
- Lohrer, A. M., M. Townsend, S. F. Hailles, I. F. Rodil, K. Cartner, D. R. Pratt, and J. E. Hewitt. 2016. “Influence of New Zealand Cockles (*Austrovenus stutchburyi*) on Primary Productivity in Sandflat-Seagrass (*Zostera muelleri*) Ecotones.” *Estuarine, Coastal and Shelf Science* 181: 238–48.
- Lohrer, A. M., M. Townsend, I. F. Rodil, J. E. Hewitt, and S. F. Thrush. 2012. “Detecting Shifts in Ecosystem Functioning: The Decoupling of Fundamental Relationships with Increased Pollutant Stress on Sandflats.” *Marine Pollution Bulletin* 64: 2761–9.
- Lundquist, C. J., C. A. Pilditch, and V. J. Cummings. 2004. “Behaviour Controls Post-Settlement Dispersal by the Juvenile Bivalves *Austrovenus stutchburyi* and *Macomona liliana*.” *Journal of Experimental Marine Biology and Ecology* 306: 51–74.
- Mangan, S., K. R. Bryan, S. F. Thrush, R. V. Gladstone-Gallagher, A. M. Lohrer, and C. A. Pilditch. 2020. “Shady Business: The Darkening of Estuaries Constrains Benthic Ecosystem Function.” *Marine Ecology Progress Series* 647: 33–48.
- McGreer, E. R. 1982. “Factors Affecting the Distribution of the Bivalve, *Macoma balthica* (L.) on a Mudflat Receiving Sewage Effluent, Fraser River Estuary, British Columbia.” *Marine Environmental Research* 7: 131–49.
- Miller, D. C., R. J. Geider, and H. L. MacIntyre. 1996. “Microphytobenthos: The Ecological Role of the ‘Secret Garden’ of Unvegetated, Shallow-Water Marine Habitats. II. Role in Sediment Stability and Shallow-Water Food Webs.” *Estuaries* 19: 202–12.
- Mook, D. H., and C. M. Hoskin. 1982. “Organic Determinations by Ignition: Caution Advised.” *Estuarine, Coastal and Shelf Science* 15: 697–9.
- Mora, F. 2017. “A Structural Equation Modeling Approach for Formalizing and Evaluating Ecological Integrity in Terrestrial Ecosystems.” *Ecological Informatics* 41: 74–90.
- Muthen, L., and B. Muthen. 2017. *Mplus User’s Guide*, 8th ed. Los Angeles, CA: Muthén & Muthén.
- Needham, H. R., C. A. Pilditch, A. M. Lohrer, and S. F. Thrush. 2010. “Habitat Dependence in the Functional Traits of *Austrohelice crassa*, a Key Bioturbating Species.” *Marine Ecology Progress Series* 414: 179–93.
- Norkko, A., A. Villnas, J. Norkko, S. Valanko, and C. Pilditch. 2013. “Size Matters: Implications of the Loss of Large Individuals for Ecosystem Function.” *Scientific Reports* 3: 2646.
- Norkko, J., J. E. Hewitt, and S. F. Thrush. 2006. “Effects of Increased Sedimentation on the Physiology of Two Estuarine Soft-Sediment Bivalves, *Austrovenus stutchburyi* and *Paphies*

- australis*." *Journal of Experimental Marine Biology and Ecology* 333: 12–26.
- Ólafsson, E. 1989. "Contrasting Influences of Suspension-Feeding and Deposit-Feeding Populations of *Macoma balthica* on Infaunal Recruitment." *Marine Ecology Progress Series* 55: 171–9.
- Petchey, O. L., A. P. Beckerman, J. O. Riede, and P. H. Warren. 2008. "Size, Foraging, and Food Web Structure." *Proceedings of the National Academy of Sciences* 105: 4191–6.
- Peterson, C. H. 1991. "Intertidal Zonation of Marine Invertebrates in Sand and Mud." *American Scientist* 79: 236–49.
- Petuha, E. T., C. J. Lundquist, and C. A. Pilditch. 2006. "Estimating Spatial Scale of Post-Settlement Transport Potential of *Macomona liliانا* on an Intertidal Sandflat." *New Zealand Journal of Marine and Freshwater Research* 40: 487–502.
- Pickett, S. T. A. 1989. "Space-for-Time Substitution as an Alternative to Long-Term Studies." In *Long-Term Studies in Ecology: Approaches and Alternatives*, edited by G. E. Likens, 110–35. New York: Springer.
- Pratt, D. R., A. M. Lohrer, C. A. Pilditch, and S. F. Thrush. 2013. "Changes in Ecosystem Function across Sedimentary Gradients in Estuaries." *Ecosystems* 17: 182–94.
- Pratt, D. R., A. M. Lohrer, S. F. Thrush, J. E. Hewitt, M. Townsend, K. Cartner, C. A. Pilditch, R. J. Harris, C. van Colen, and I. F. Rodil. 2015. "Detecting Subtle Shifts in Ecosystem Functioning in a Dynamic Estuarine Environment." *PLoS One* 10: e0133914.
- Pratt, D. R., C. A. Pilditch, D. Lohrer, and S. F. Thrush. 2014. "The Effects of Short-Term Increases in Turbidity on Sandflat Microphytobenthic Productivity and Nutrient Fluxes." *Journal of Sea Research* 92: 170–7.
- Pridmore, R. D., S. F. Thrush, J. E. Hewitt, and D. S. Roper. 1990. "Macrobenthic Community Composition of 6 Intertidal Sandflats in Manukau Harbor, New Zealand." *New Zealand Journal of Marine and Freshwater Research* 24: 81–96.
- Pridmore, R. D., S. F. Thrush, R. J. Wilcock, T. J. Smith, J. E. Hewitt, and V. J. Cummings. 1991. "Effect of the Organochlorine Pesticide Technical Chlordane on the Population Structure of Suspension and Deposit Feeding Bivalves." *Marine Ecology Progress Series* 76: 261–71.
- Probert, P. 1984. "Disturbance, Sediment Stability, and Trophic Structure of Soft-Bottom Communities." *Journal of Marine Research* 42: 893–921.
- Rhoads, D., and L. Boyer. 1982. "The Effects of Marine Benthos on Physical Properties of Sediments: A Successional Perspective." In *Animal-Sediment Relations*, edited by P. McCall and M. Tevesz, 3–52. New York: Springer.
- Rhoads, D., and J. Germano. 1982. "Characterization of Organism–Sediment Relationships Using Sediment Profile Imaging: An Efficient Method of Remote Ecological Monitoring of the Seafloor (REMOTS™ System)." *Marine Ecology Progress Series* 8: 115–28.
- Robertson, B. P., J. P. A. Gardner, and C. Savage. 2015. "Macrobenthic–Mud Relations Strengthen the Foundation for Benthic Index Development: A Case Study from Shallow, Temperate New Zealand Estuaries." *Ecological Indicators* 58: 161–74.
- Rodil, I. F., A. M. Lohrer, L. D. Chiaroni, J. E. Hewitt, and S. F. Thrush. 2011. "Disturbance of Sandflats by Thin Terrigenous Sediment Deposits: Consequences for Primary Production and Nutrient Cycling." *Ecological Applications* 21: 416–26.
- Rodil, I. F., A. M. Lohrer, J. E. Hewitt, M. Townsend, S. F. Thrush, and M. Carbines. 2013. "Tracking Environmental Stress Gradients Using Three Biotic Integrity Indices: Advantages of a Locally-Developed Traits-Based Approach." *Ecological Indicators* 34: 560–70.
- Roper, D. S., R. D. Pridmore, and S. F. Thrush. 1992a. "Population Biology of *Tellina liliانا* in Manukau Harbour, New Zealand." *New Zealand Journal of Marine and Freshwater Research* 26: 385–92.
- Roper, D. S., R. D. Pridmore, and S. F. Thrush. 1992b. "Recruitment to the Macrobenthos of *Macomona liliانا* (Bivalvia: Tellinidae) in Manukau Harbour, New Zealand." *New Zealand Journal of Marine and Freshwater Research* 26: 385–92.
- Rowden, A., K. Berkenbusch, P. Brewin, J. Dalen, K. Neill, W. Nelson, M. Oliver, et al. 2012. "Review of the Marine Soft-Sediment Assemblages of New Zealand." New Zealand Aquatic Environment and Biodiversity Report No. 96. 165 pp. https://fs.fish.govt.nz/Doc/23030/AEBR_96.pdf.ashx.
- Rullens, V., A. M. Lohrer, M. Townsend, and C. A. Pilditch. 2019. "Ecological Mechanisms Underpinning Ecosystem Service Bundles in Marine Environments—A Case Study for Shellfish." *Frontiers in Marine Science* 6: 409.
- Sandwell, D. R., C. A. Pilditch, and A. M. Lohrer. 2009. "Density Dependent Effects of an Infaunal Suspension-Feeding Bivalve (*Austrovenus stutchburyi*) on Sandflat Nutrient Fluxes and Microphytobenthic Productivity." *Journal of Experimental Marine Biology and Ecology* 373: 16–25.
- Sartory, D. 1982. *Spectrophotometric Analysis of Chlorophyll a in Freshwater Phytoplankton*. Pretoria: Hydrological Research Institute, Department of Environmental Affairs.
- Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. van Nes, M. Rietkerk, and G. Sugihara. 2009. "Early-Warning Signals for Critical Transitions." *Nature* 461: 53–9.
- Smith, A. M., A. C. L. Wood, M. F. A. Liddy, A. E. Shears, and C. I. Fraser. 2010. "Human Impacts in an Urban Port: The Carbonate Budget, Otago Harbour, New Zealand." *Estuarine, Coastal and Shelf Science* 90: 73–9.
- Sorte, C. J. B., A. Fuller, and M. E. S. Bracken. 2010. "Impacts of a Simulated Heat Wave on Composition of a Marine Community." *Oikos* 119: 1909–18.
- Stephenson, F., R. V. Gladstone-Gallagher, R. H. Bulmer, S. F. Thrush, and J. E. Hewitt. 2022. "Inclusion of Biotic Interactions Improve Predictions of Environmental Niche Models." *Diversity and Distributions* 28: 1373–90.
- Sundback, K., and A. Miles. 2002. "Role of Microphytobenthos and Denitrification for Nutrient Turnover in Embayments with Floating Macroalgal Mats: A Spring Situation." *Aquatic Microbial Ecology* 30: 91–101.
- Sundback, K., A. Miles, S. Hulth, L. Pihl, P. Engstrom, E. Selander, and A. Svenson. 2003. "Importance of Benthic Nutrient Regeneration during Initiation of Macroalgal Blooms in Shallow Bays." *Marine Ecology Progress Series* 246: 115–26.
- Swales, A., R. Bell, and D. Lohrer. 2020. "Chapter 6: Estuaries and Lowland Brackish Habitats." In *Coastal Systems and Sea Level Rise: What to Look for in the Future*, edited by C. Hendtlass,

- S. Morgan, and D. Neale, 68. Wellington: New Zealand Coastal Society Special Publication.
- Thrush, S. F., V. J. Cummings, P. K. Dayton, R. Ford, J. Grant, J. E. Hewitt, A. H. Hines, et al. 1997. "Matching the Outcome of Small-Scale Density Manipulation Experiments with Larger Scale Patterns: An Example of Bivalve Adult/Juvenile Interactions." *Journal of Experimental Marine Biology and Ecology* 216: 153–69.
- Thrush, S. F., and P. K. Dayton. 2002. "Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity." *Annual Review of Ecology and Systematics* 33: 449–73.
- Thrush, S. F., J. E. Hewitt, V. Cummings, J. I. Ellis, C. Hatton, A. Lohrer, and A. Norkko. 2004. "Muddy Waters: Elevating Sediment Input to Coastal and Estuarine Habitats." *Frontiers in Ecology and the Environment* 2: 299–306.
- Thrush, S. F., J. E. Hewitt, V. J. Cummings, M. O. Green, G. A. Funnell, and M. R. Wilkinson. 2000. "The Generality of Field Experiments: Interactions between Local and Broad-Scale Processes." *Ecology* 81: 399–415.
- Thrush, S. F., J. E. Hewitt, M. Gibbs, C. Lundquist, and A. Norkko. 2006. "Functional Role of Large Organisms in Intertidal Communities: Community Effects and Ecosystem Function." *Ecosystems* 9: 1029–40.
- Thrush, S. F., J. E. Hewitt, R. V. Gladstone-Gallagher, C. Savage, C. Lundquist, T. O'Meara, A. Vieillard, et al. 2020. "Cumulative Stressors Reduce the Self-Regulating Capacity of Coastal Ecosystems." *Ecological Applications* 31: e02223.
- Thrush, S. F., J. E. Hewitt, C. W. Hickey, and S. Kelly. 2008. "Multiple Stressor Effects Identified from Species Abundance Distributions: Interactions between Urban Contaminants and Species Habitat Relationships." *Journal of Experimental Marine Biology and Ecology* 366: 160–8.
- Thrush, S. F., J. E. Hewitt, A. Lohrer, and L. D. Chiaroni. 2013. "When Small Changes Matter: The Role of Cross-Scale Interactions between Habitat and Ecological Connectivity in Recovery." *Ecological Applications* 23: 226–38.
- Thrush, S. F., J. E. Hewitt, and A. M. Lohrer. 2012. "Interaction Networks in Coastal Soft-Sediments Highlight the Potential for Change in Ecological Resilience." *Ecological Applications* 22: 1213–23.
- Thrush, S. F., J. E. Hewitt, A. Norkko, P. E. Nicholls, G. A. Funnell, and J. I. Ellis. 2003. "Habitat Change in Estuaries: Predicting Broad-Scale Responses of Intertidal Macrofauna to Sediment Mud Content." *Marine Ecology Progress Series* 263: 101–12.
- Thrush, S. F., J. E. Hewitt, R. D. Pridmore, and V. J. Cummings. 1996. "Adult/Juvenile Interactions of Infaunal Bivalves: Contrasting Outcomes in Different Habitats." *Marine Ecology Progress Series* 132: 83–92.
- Thrush, S. F., R. D. Pridmore, and J. E. Hewitt. 1996. "Impacts on Soft-Sediment Macrofauna: The Effects of Spatial Variation on Temporal Trends." In *Detecting Ecological Impacts: Concepts and Applications in Coastal Habitats*, edited by R. J. Schmitt and C. W. Osenberg, 49–66. San Diego, CA: Academic Press.
- Thrush, S. F., R. D. Pridmore, J. E. Hewitt, and V. J. Cummings. 1992. "Adult Infauna as Facilitators of Colonization on Intertidal Sandflats." *Journal of Experimental Marine Biology and Ecology* 159: 253–65.
- Topçu, N. E., E. Turgay, R. E. Yardımcı, B. Topaloğlu, A. Yüksek, T. M. Steinum, S. Karataş, and B. Öztürk. 2019. "Impact of Excessive Sedimentation Caused by Anthropogenic Activities on Benthic Suspension Feeders in the Sea of Marmara." *Journal of the Marine Biological Association of the United Kingdom* 99: 1075–86.
- Van Colen, C., S. F. Thrush, S. Parkes, R. Harris, S. A. Woodin, D. S. Wethey, C. A. Pilditch, J. E. Hewitt, A. M. Lohrer, and M. Vincx. 2014. "Bottom-Up and Top-Down Mechanisms Indirectly Mediate Interactions between Benthic Biotic Ecosystem Components." *Journal of Sea Research* 98: 42–8.
- Van Colen, C., S. F. Thrush, M. Vincx, and T. Ysebaert. 2013. "Conditional Responses of Benthic Communities to Interference from an Intertidal Bivalve." *PLoS One* 8: e65861.
- van de Koppel, J., P. M. J. Herman, P. Thoolen, and C. H. R. Heip. 2001. "Do Alternate Stable States Occur in Natural Ecosystems? Evidence from a Tidal Flat." *Ecology* 82: 3449–61.
- van der Heide, T., E. H. van Nes, M. M. van Katwijk, H. Olff, and A. J. P. Smolders. 2011. "Positive Feedbacks in Seagrass Ecosystems—Evidence from Large-Scale Empirical Data." *PLoS One* 6: e16504.
- Volkenborn, N., D. M. Robertson, and K. Reise. 2009. "Sediment Destabilizing and Stabilizing Bio-Engineers on Tidal Flats: Cascading Effects of Experimental Exclusion." *Helgoland Marine Research* 63: 27–35.
- Whitlatch, R. B., A. H. Hines, S. F. Thrush, J. E. Hewitt, and V. Cummings. 1997. "Benthic Faunal Responses to Variations in Patch Density and Patch Size of a Suspension-Feeding Bivalve." *Journal of Experimental Marine Biology and Ecology* 216: 171–89.
- Woodin, S., and J. Jackson. 1979. "Interphyletic Competition among Marine Benthos." *American Zoologist* 19: 1029–43.
- Woodin, S. A., D. S. Wethey, J. E. Hewitt, and S. F. Thrush. 2012. "Small Scale Terrestrial Clay Deposits on Intertidal Sandflats: Behavioral Changes and Productivity Reduction." *Journal of Experimental Marine Biology and Ecology* 413: 184–91.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Douglas, Emily J., Judi Hewitt, Andrew M. Lohrer, and Fabrice Stephenson. 2023. "Changing Intra- and Interspecific Interactions across Sedimentary and Environmental Stress Gradients." *Ecosphere* 14(1): e4373. <https://doi.org/10.1002/ecs2.4373>