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Climate-related drivers of estuarine macrobenthic functional redundancy and resilience

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ABSTRACT

Elevated anthropogenic CO_2 emissions are warming the planet, although our understanding of how climate-related changes manifest locally remains poor. In estuaries, rising air and sea surface temperatures, increased sediment loading, and climate-related changes (e.g., cyclones, heatwaves, droughts) can collectively influence tidal flat biota and the key ecosystem functions they mediate. Here, we used long-term data from six sites in a New Zealand estuary (all sampled quarterly for 22 years) to evaluate tidal flat macroinvertebrate changes and responses of five functional diversity metrics (i.e., Functional Richness, Evenness, Dispersion, Divergence, and Redundancy) to shifting environmental conditions. Sea surface temperature (satellite SST records), sediment organic matter content (OM), and bed sediment muddiness all increased significantly at all sites from 2000 to 2022. The individual effects of these environmental drivers on functional diversity metrics were mixed, but net trends in Functional Richness and Functional Redundancy indicated increasing levels of community resilience over time. Heat spikes can cause thermal stress, but gradual warming may elevate metabolic rates and accelerate reactions such as photosynthesis. The positive effects on increased food supply (OM) could have outweighed negative influences of increasing mud, generating the net trends in our data. Overall, our research suggests that some estuarine soft-sediment macroinvertebrate communities, based on the analysis of functional diversity metrics, are becoming increasingly resilient and adaptable, rather than increasingly depauperate and functionally impacted, as climate change strengthens.

1. Introduction

Increasing greenhouse gas emissions coincident with exponential human population growth and industrialisation are linked to global warming and impacts to Earth's ecosystems. 2023 was determined to be the hottest year in the modern record, and eighteen of the nineteen warmest years on record have occurred since 2000 [1–3].

Earth's oceans are absorbing heat and atmospheric CO_2 [4–6]. Despite the capacity of the oceans to buffer these stressors [5,7], temperatures and CO_2 concentrations in seawater are rising worldwide and manifesting as marine heat waves and ocean acidification [5,6,8], which are directly impacting marine species and ecosystems, e.g., increasing the extent and intensity of coral bleaching [9,10], reducing kelp forest cover [11–13], disrupting food webs [14–17], and shifting the distributions of fisheries species [18–21].

Estuarine ecosystems are water bodies located at the land-sea interface. These ecosystems experience wider temperature and pH fluctuations than open ocean environments as estuaries are shallower and water movement is more restricted [22–24]. Rising air temperatures are a primary driver of widely observed increases in estuarine water temperature [23,25,26], which may in turn increase effects of hypoxia/anoxia [27–29], pathogens and diseases [30], and harmful algal blooms [27,31].

In addition to rising temperatures, estuaries have greater exposure to other climate-related changes. For example, the shape, depth, salinity gradient, and volume of estuaries will change with climate-associated increases in mean sea level [32–34] with the potential to influence hydrodynamics, productivity, and the distribution of habitats. Furthermore, the frequency and intensity of storms is predicted to increase with ocean warming [35–37], with storm-associated rainfall likely to increase the erosion of soils from coastal catchments and subsequent loading of fine sediments, pollutants, nutrients, and organic matter to estuaries [27,38–40]. Increased suspended fine sediment concentrations and bed sediment muddiness are well-documented major threats to estuarine biodiversity and ecosystem function [41–45].

Despite adverse impacts and an undeniable need to control

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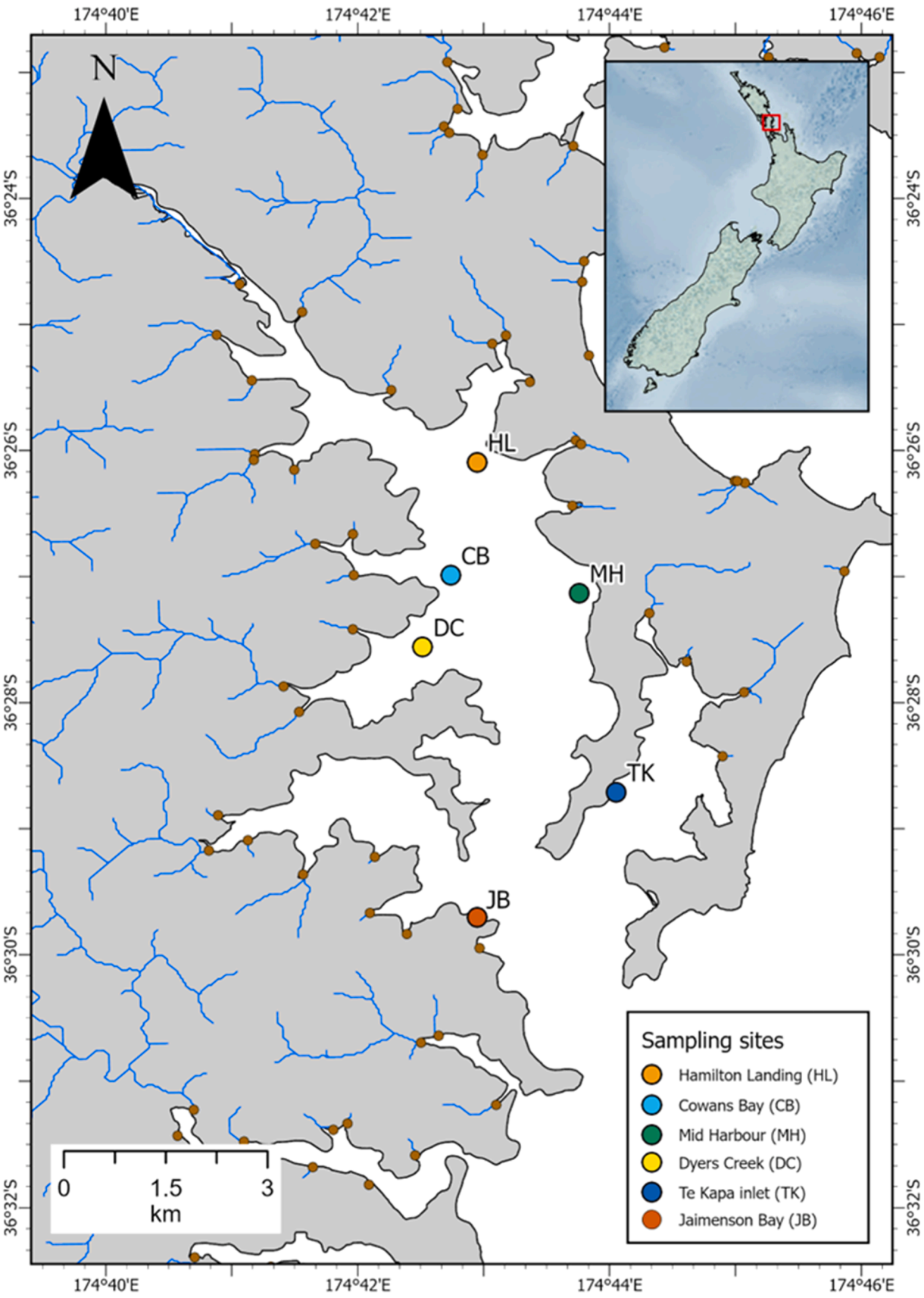

Fig. 1. Mahurangi Harbour, North Island, New Zealand, and the six macroinvertebrate sampling sites. Blue lines show the river and small gold points show the rivers outlets.

Table 1
Summary of the main characteristics of each sampling site in Mahurangi Harbour (New Zealand) analysed in this study. *No sampling was carried out in 2012–2015 and 2019–2021.

Site	Site ID	Macrobenthic time series	Sampling frequency	Total number of macrobenthic core replicates (n)	Total abundance of all taxa collected (ind/core)	Total mean abundance of all taxa collected (ind/core)	Total number of species collected (Richness)	Total mean number of species collected (Richness)
Hamilton Landing	HL	2000–2022	3 months	984	127,504	130	128	12
Cowans Bay	CB	2000–2022*	3 months	660	47,035	71	122	12
Mid Harbour	MH	2000–2022	3 months	1092	73,661	67	163	13
Dyers Creek	DC	2005–2022	3 months	816	61,181	75	121	13
Te Kapa inlet	TK	2000–2022	3 months	1092	95,634	88	150	13
Jaimenson Bay	JB	2000–2022	3 months	1104	113,096	102	235	18

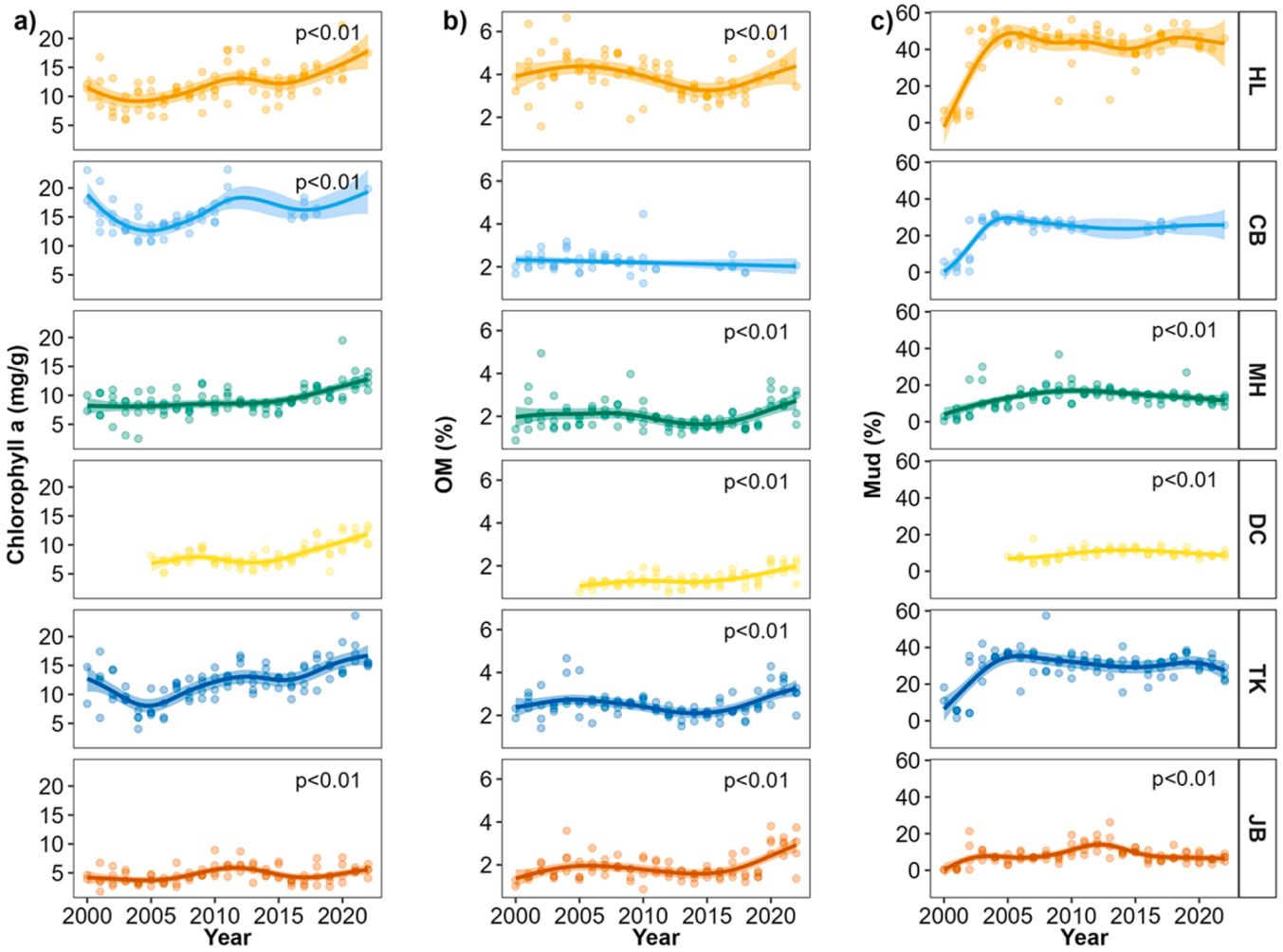

Fig. 2. Summary results of GAMs by site in Mahurangi Harbour. Partial residual plots indicating the trend of (a) Chlorophyll a (mg/g), (b) Organic Matter content in sediment (%), (c) Mud content in sediment (%) over time. Coloured solid lines show the locally estimated smoothing trends; shading shows the 95 % confidence intervals, and coloured solid points show the residual values. Significant interactions are showed as noted p values.

greenhouse gas emissions globally, the effects of climate-related changes will not be negative for all biota and ecosystems. Almost all chemical reactions are faster at higher temperature, including biologically mediated reactions within cells [46,47]. Thus, for ectothermic organisms in the marine realm, the elevation of metabolic rates with warming could have positive effects on key processes and groups of organisms [46,48–50]. Rates of photosynthesis (use of sunlight energy to fix carbon), for example, are generally predicted to increase with warming [51, 52]. Nevertheless, beyond an optimal thermal range, further warming can cause metabolic depression, where the metabolic rate levels off or even decreases [53–55]. This occurs because high temperatures can induce physiological and molecular stress, resulting in organisms actively or passively suppressing energy-consuming processes to prevent cellular damage and conserve resources [53–55].

Benthic macroinvertebrate communities (comprised of ectotherms organisms that will respond to variations in temperature) are widely recognised as sensitive indicators of estuarine health and function [56–58] and are sampled and monitored in estuaries worldwide [29,56,

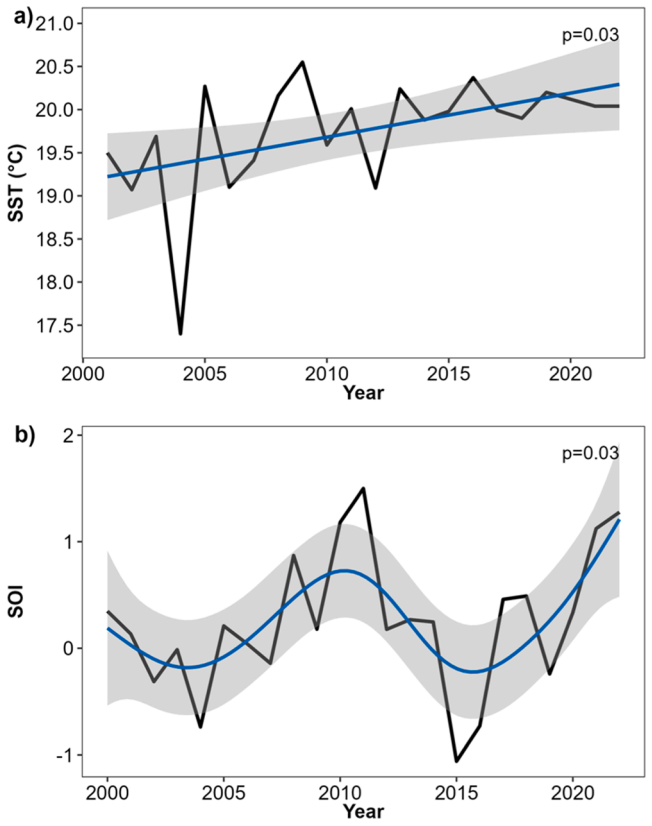

Fig. 3. Summary results of GAMs by site in Mahurangi Harbour. Partial residual plots indicating the trend of Sea Surface Temperature (°C, recorded in austral autumn – April) and Southern Oscillation Index (SOI >1 La Niña phase, SOI < -1.0 El Niño phase) over time. Coloured blue lines show the locally estimated smoothing trends and shading shows the 95 % confidence intervals. Significant interactions are showed as noted p values.

Table 2
Summary results of the GAM analyses assessing the environmental trends over time at each site. Chl a: Chlorophyll a, OM: Organic matter content in sediment, Mud: Mud content in sediment, SST: Sea Surface Temperature, SOI: Southern Oscillation Index.

	Site	p value	R^2	Deviance explained	AIC	Slope
Chl a						
	HL	0.00000065	0.40	0.434	388.0	0.288
	CB	0.00000870	0.48	0.530	240.0	0.022
	MH	0	0.36	0.382	379.0	0.208
	DC	0	0.57	0.597	246.0	0.296
	TK	0	0.53	0.559	419.0	0.180
	JB	0.00021400	0.26	0.301	306.0	0.063
OM						
	HL	0.00244000	0.20	0.235	209.0	0.022
	CB	0.30100000	0.01	0.025	77.2	-0.014
	MH	0.00249000	0.18	0.220	172.0	0.035
	DC	0.00000096	0.40	0.429	37.5	0.054
	TK	0.00009740	0.26	0.294	151.0	0.040
	JB	0.00000085	0.35	0.382	138.0	0.071
Mud						
	HL	0	0.60	0.628	596.0	2.070
	CB	0	0.76	0.792	318.0	1.170
	MH	0.00000519	0.30	0.323	550.0	0.345
	DC	0.00009330	0.29	0.329	312.0	0.114
	TK	0	0.43	0.462	616.0	0.955
	JB	0.00000077	0.39	0.432	503.0	0.282
SST	All	0.02960000	0.19	0.226	43.2	0.051
SOI	All	0.03582000	0.44	56.300	41.1	0.026

59,60]. Many macrofauna rely directly or indirectly on microphytobenthos as a food resource [61,62], and climate-related changes in estuaries may stimulate diatoms [63–66], the dominant component of microphytobenthos. The movements and feeding behaviours of macrofauna are central to their roles in soft-sediment ecosystems (e.g., as bioturbators, bioirrigators, sediment stabilisers/destabilisers) [62], therefore, climate-related changes in activity rates and food supply could alter community dynamics.

Analyses of estuarine sediment and macroinvertebrate community time-series data can provide insights into the responses of estuaries to climate-related change (e.g., [67,68]). Yet, analyses of responses to multiple climate-related stressors simultaneously, and testing of the linkages to functioning and resilience, are generally lacking.

Functional diversity, defined as the components of biodiversity that influence how an ecosystem operates or functions (e.g., functional traits), has been proposed as a key measure for assessing relationships between biodiversity, the roles of organisms in communities, and links to ecosystem properties such as resistance and resilience to stressors [58,69–71]. Functional diversity has advantages over classical measures of diversity in terms of understanding of large-scale ecosystem processes as it includes knowledge of the components of biodiversity that influence ecological processes and ecosystem functioning [70,72–75]. Several metrics have been developed to quantify functional diversity, and functional diversity has several facets (e.g., functional richness, functional evenness, functional divergence, functional dispersion, and functional redundancy). The multiple facets provide versatility and complementary ways of describing the distribution of traits in a community, enabling the evaluation of within- and among-assemblage components [58,71,76–78]. Functional richness and functional redundancy—the degree to which species perform similar functional roles in a community, helping the system to maintain functionality should some species be lost—are particularly useful for gauging the resilience of ecosystems to stressors.

In estuarine ecosystems, several investigations have assessed the relationship between biodiversity and ecosystem functioning using various functional diversity metrics (e.g., [79–83]). However, empirical studies assessing long-term functional patterns in estuarine ecosystems are scarce, with the majority of the studies based on short-term assessments, manipulative experimentation, or modelling ([58,84–86]. Thus, our ability to predict changes in estuarine functionality and assist conservation and management decisions given climate change remains limited.

Here, we leveraged existing high-quality estuarine time-series data (>20 years of quarterly sampling at six sites in a well-studied southern hemisphere estuary) to investigate how estuarine macrobenthic functioning has changed over time. We focused on estuarine macrobenthic fauna as these organisms are central to ecosystem functioning, e.g., regulating fluxes of energy and matter [87,88], bioturbating sediments [62,89], and promoting sediment oxygenation [90,91].

Along with the macroinvertebrates, time-series data on sediment muddiness (linked to sediment loading from the land), sediment chlorophyll *a* content (i.e., microphytobenthos abundance), organic matter content in sediment, sea-surface temperatures, and Southern Oscillation Index, allowing us to explore the significance of multiple climate-related drivers simultaneously. Specifically, we investigated macrobenthic functional changes over time using a suite of five different functional metrics, and evaluated the relationships between the macrobenthic functional metrics and multiple environmental drivers. A primary motivation for the study was to determine the simultaneous (net) effects of multiple climate-related drivers on estuarine macrobenthic functional richness (as proxy of ecological resilience), evenness, divergence, dispersion and redundancy.

We hypothesised that macrobenthic functional metrics are influenced over the long term by interacting environmental drivers such as

Table 3
Summary results of the GAM analyses assessing Functional Richness. Chl a: Chlorophyll a; Mud: Mud content in sediment; OM: Organic content in sediment; SST: Sea Surface Temperature; SOI: Southern Oscillation Index, Significant interactions are highlighted in bold.

Functional Richness				
	edf	**Ref.df**	**F**	**P-value**
a) HL				
s(Year)	1.598	1.963	2.675	0.071847
s(SOI)	1.917	2.421	2.28	0.116123
s(SST)	2.866	3.482	7.055	**0.000173**
s(Chla)	1	1.001	0.7	0.405598
s(Mud)	2.907	3.61	2.209	0.080356
s(OM)	1.533	1.897	0.328	0.679693
		R^2=0.43	Dev. Exp. = 51.8 %	
b) CB				
s(Year)	2.364	2.951	7.009	**0.000447**
s(SOI)	1.175	1.327	0.792	0.485116
s(SST)	1	1	8.004	**0.007005**
s(Chla)	1	1	0.495	0.485197
s(Mud)	1	1	1.122	0.295311
s(OM)	1	1	0.124	0.726675
		R^2=0.38	Dev. Exp. = 47.3 %	
c) MH				
s(Year)	8.005	8.709	32.203	**0.000001**
s(SOI)	2.263	2.843	2.276	0.113776
s(SST)	2.25	2.754	2.201	0.074733
s(Chla)	1	1.001	0.074	0.786749
s(Mud)	3.642	4.568	5.62	**0.000387**
s(OM)	2.336	2.921	1.235	0.260976
		R^2=0.85	Dev. Exp. = 88.5 %	
d) DC				
s(Year)	3.568	4.412	6.129	**0.000264**
s(SOI)	1	1	0.827	0.367066
s(SST)	1.982	2.464	3.841	**0.025953**
s(Chla)	1.275	1.487	1.335	0.304963
s(Mud)	3.129	3.946	1.935	0.154609
s(OM)	1.582	1.956	3.943	**0.018097**
		R^2=0.55	Dev. Exp. = 64.2 %	
e) TK				
s(Year)	3.693	4.609	1.869	0.1172
s(SOI)	1.852	2.329	0.761	0.5816
s(SST)	1	1	5.82	**0.0183**
s(Chla)	1.203	1.376	0.586	0.4178
s(Mud)	1	1	0.04	0.843
s(OM)	2.16	2.705	3.476	**0.0291**
		R^2=0.22	Dev. Exp. = 32.5 %	
d) JB				
s(Year)	5.026	6.173	14.723	**0.000001**
s(SOI)	1.225	1.41	0.09	0.7937
s(SST)	1	1	2.958	0.0894
s(Chla)	1.807	2.287	1.686	0.2092
s(Mud)	1	1	0.723	0.3978
s(OM)	1	1	0.114	0.7362
		R^2=0.59	Dev. Exp. = 64.6 %	

Table 4
Summary results of the GAM analyses assessing Functional Evenness. Chl a: Chlorophyll a; Mud: Mud content in sediment; OM: Organic content in sediment; SST: Sea Surface Temperature; SOI: Southern Oscillation Index, Significant interactions are highlighted in bold.

Functional Evenness				
	edf	**Ref.df**	**F**	**P-value**
a) HL				
s(Year)	4.805	5.962	8.314	**0.000001**
s(SOI)	1	1	0.329	0.5679
s(SST)	1.327	1.588	4.662	**0.0328**
s(Chla)	1	1	0.319	0.5744
s(Mud)	1.404	1.687	3.058	0.068
s(OM)	1	1	0.009	0.9231
		R^2=0.52	Dev. Exp. = 58.5 %	
b) CB				
s(Year)	2.655	3.313	4.024	**0.0123**
s(SOI)	1	1	0.01	0.9223
s(SST)	1	1	0.9	0.3479
s(Chla)	1	1	0.402	0.5295
s(Mud)	1	1	0.356	0.5539
s(OM)	1.717	2.139	1.257	0.2673
		R^2=0.23	Dev. Exp. = 35.9 %	
c) MH				
s(Year)	3.218	4.052	16.81	**0.000206**
s(SOI)	1	1	1.362	0.2469
s(SST)	1	1	0.198	0.6578
s(Chla)	1	1	2.28	0.1351
s(Mud)	1	1	2.449	0.1217
s(OM)	1	1	7.49	**0.0077**
		R^2=0.50	Dev. Exp. = 54.9 %	
d) DC				
s(Year)	4.125	5.113	2.249	0.06273
s(SOI)	1	1	7.952	**0.00659**
s(SST)	1	1	0.577	0.45088
s(Chla)	1.931	2.406	1.4	0.22497
s(Mud)	1	1	3.52	0.06575
s(OM)	1	1	8.239	**0.00574**
		R^2=0.48	Dev. Exp. = 56.2 %	
e) TK				
s(Year)	2.561	3.21	3.041	**0.030563**
s(SOI)	1.531	1.896	2.028	0.193403
s(SST)	1	1.001	14.92	**0.000232**
s(Chla)	1	1	0.743	0.391308
s(Mud)	1	1	3.636	0.060272
s(OM)	1	1	0.943	0.334563
		R^2=0.23	Dev. Exp. = 30.6 %	
d) JB				
s(Year)	4.864	5.989	11.303	**0.000206**
s(SOI)	1.328	1.582	0.175	0.706
s(SST)	1.326	1.586	1.56	0.31
s(Chla)	1	1	0.943	0.334
s(Mud)	1.433	1.748	1.627	0.174
s(OM)	1	1	1.676	0.199
		R^2=0.43	Dev. Exp. = 50.9 %	

sediment chlorophyll a (positive), organic matter (negative), sediment mud content (negative), and sea surface temperature (positive), reflecting the combined influence of food availability, sediment characteristics, and thermal conditions.

2. Materials and methods

2.1. Study area

The study was carried out in Mahurangi Harbour (Fig. 1). Mahurangi is a 24.7 km^2 harbour located on the east coast in the North Island of New Zealand [92,93], with intertidal flats ranging from fine muddy sediments at the head of the harbour to coarse sands near the mouth. Pastoral farming, lifestyle blocks, and forestry occur in the catchment [92–94]. Macrobenthic data were collected from six sites (HL, CB, MH, DC, TK, and JB; Table 1) throughout Mahurangi Harbour over a period of 22 years (2000–2022). These six sites were positioned along a gradient from inner to outer estuary. The estuary has a ~3 m tidal range and twice-daily tidal flushing that thoroughly mixes the water column, therefore, even the innermost arms of this estuary are generally nearly full-strength seawater (>32 PSU) at high tide. None of the sites were located in tidal creeks that might experience lower salinity seawater at low tide after significant rain events.

2.2. Data collection

2.2.1. Biological data

Macrobenthic data collection, processing of samples, sorting, and identifications followed standard protocols for New Zealand [95], with strict quality assurance, quality control procedures, and taxonomic harmonization [95–98], providing high confidence in the validity of data comparisons over time. Samples were collected quarterly from 2000–2022 (Table 1). Briefly, 12 replicate sediment samples for assessing macrobenthic fauna were collected during low tide at each site

Table 5
Summary results of the GAM analyses assessing Functional Divergence. Chl a: Chlorophyll a; Mud: Mud content in sediment; OM: Organic content in sediment; SST: Sea Surface Temperature; SOI: Southern Oscillation Index, Significant interactions are highlighted in bold.

Functional Divergence				
	edf	**Ref.df**	**F**	**P-value**
a) HL				
s(Year)	1	1	0.181	0.67197
s(SOI)	1	1	0.012	0.91292
s(SST)	2.626	3.241	5.618	**0.00135**
s(Chla)	1	1	1.46	0.23093
s(Mud)	1.214	1.394	0.844	0.30228
s(OM)	1	1	0.19	0.66416
		R^2=0.18	Dev. Exp. = 26.7 %	
b) CB				
s(Year)	1	1	2.401	0.1282
s(SOI)	1	1	1.51	0.2253
s(SST)	1	1	4.472	**0.0399**
s(Chla)	1	1	0.031	0.8608
s(Mud)	1.454	1.783	1.552	0.2895
s(OM)	1	1	0.34	0.5627
		R^2=0.06	Dev. Exp. = 18 %	
c) MH				
s(Year)	6.067	7.212	18.566	**0.000206**
s(SOI)	3.244	4.025	1.077	0.354
s(SST)	1	1	2.274	0.136
s(Chla)	1	1	0.581	0.449
s(Mud)	3.399	4.257	1.638	0.169
s(OM)	2.182	2.737	0.51	0.539
		R^2=0.71	Dev. Exp. = 77 %	
d) DC				
s(Year)	1	1	2.302	0.13468
s(SOI)	1.492	1.835	0.724	0.56802
s(SST)	1	1	10.846	**0.00169**
s(Chla)	1	1	0.002	0.9692
s(Mud)	3.583	4.482	7.513	**0.00004**
s(OM)	1	1	2.015	0.16111
		R^2=0.50	Dev. Exp. = 56.8 %	
e) TK				
s(Year)	1	1	7.714	**0.00688**
s(SOI)	1	1	0.502	0.48088
s(SST)	2.061	2.575	1.029	0.29252
s(Chla)	1	1	0.004	0.9512
s(Mud)	1	1	0.736	0.3937
s(OM)	1.894	2.38	1.275	0.32952
		R^2=0.16	Dev. Exp. = 24.2 %	
d) JB				
s(Year)	6.61	7.777	3.442	**0.00184**
s(SOI)	1	1	3.998	**0.04913**
s(SST)	1	1	4.077	**0.04696**
s(Chla)	1	1	0.002	0.96673
s(Mud)	1	1	0.327	0.56915
s(OM)	1	1	1.146	0.28777
		R^2=0.31	Dev. Exp. = 40.9 %	

Table 6
Summary results of the GAM analyses assessing Functional Dispersion. Chl a: Chlorophyll a; Mud: Mud content in sediment; OM: Organic content in sediment; SST: Sea Surface Temperature; SOI: Southern Oscillation Index, Significant interactions are highlighted in bold.

Functional Dispersion				
	edf	**Ref.df**	**F**	**P-value**
a) HL				
s(Year)	3.712	4.651	8.189	**0.000009**
s(SOI)	1	1.001	0.443	0.5083
s(SST)	2.673	3.281	2.58	**0.0527**
s(Chla)	1.535	1.892	0.403	0.6911
s(Mud)	1.555	1.894	1.372	0.3164
s(OM)	1.228	1.414	0.467	0.4716
		R^2=0.52	Dev. Exp. = 59.2 %	
b) CB				
s(Year)	1	1	14.015	**0.000503**
s(SOI)	1	1	0.003	0.95609
s(SST)	1.368	1.656	0.588	0.641609
s(Chla)	1	1	0.446	0.507413
s(Mud)	1	1	1.161	0.28683
s(OM)	1	1	0.214	0.645497
		R^2=0.35	Dev. Exp. = 43 %	
c) MH				
s(Year)	6.494	7.632	18.981	**0.000206**
s(SOI)	1.536	1.895	0.774	0.534
s(SST)	1	1	1.346	0.25
s(Chla)	1	1	0.17	0.681
s(Mud)	1	1	6.078	**0.016**
s(OM)	1	1	2.261	0.137
		R^2=0.67	Dev. Exp. = 71.9 %	
d) DC				
s(Year)	1	1	46.91	**0.000206**
s(SOI)	1.527	1.881	3.197	**0.0378**
s(SST)	1	1	1.402	0.2413
s(Chla)	1	1	0.473	0.4944
s(Mud)	3.571	4.462	8.597	**0.00002**
s(OM)	2.081	2.607	1.264	0.2527
		R^2=0.79	Dev. Exp. = 82.5 %	
e) TK				
s(Year)	1.359	1.624	1.466	0.1675
s(SOI)	1	1	1.9	0.1721
s(SST)	1.59	1.98	2.492	0.0759
s(Chla)	1	1	1.035	0.3122
s(Mud)	1.403	1.707	0.191	0.8299
s(OM)	2.611	3.284	1.543	0.1893
		R^2=0.12	Dev. Exp. = 22.1 %	
d) JB				
s(Year)	7.905	8.667	14.589	**0.000206**
s(SOI)	2.048	2.608	2.791	**0.05252**
s(SST)	1	1	7.703	**0.00698**
s(Chla)	1	1	0.014	0.90484
s(Mud)	1	1	0.073	0.78784
s(OM)	1	1	1.529	0.22015
		R^2=0.62	Dev. Exp. = 68.1 %	

from mid-intertidal areas on each occasion (approximately every 3 months) across all years using a hand-held PVC corer (13 cm diameter by 15 cm depth), sieved through a 0.5 mm mesh size, and preserved in 70 % isopropanol. Benthic macrofauna were sorted, identified to the lowest possible taxonomic level (usually genus or species), and counted.

2.2.2. Environmental drivers

To evaluate the relationship between macrobenthic functional metrics and environmental drivers, we compiled data on five different environmental variables with the potential to affect estuarine ecosystems: three in situ sedimentary variables, an index of broad climatological conditions, and an oceanic variable. Respectively, these variables were sediment Chlorophyll *a* content (Chl *a*, mg/g), sediment Organic Matter content (OM, %), sediment Mud content (Mud, % dry weight of silt and clay particles <63 um), nearest monthly Southern Oscillation Index value (SOI), and downscaled satellite-derived Sea Surface Temperature (SST, degrees Celsius).

At the same sites and times as macrofaunal sampling, sediment samples were collected for Chl *a*, OM, and sediment grain size using a smaller PVC corer (26 mm diameter, 20 mm deep core). Each replicate for Chl *a*, OM, and sediment grain size were an amalgam of six cores collected at positions spanning the site [41,79,99].

Analytical procedures used for Chl *a*, OM, and Mud were specific to each. Chl *a* was extracted from freeze dried sediments by boiling in 90 % ethanol. The extract was measured spectrophotometrically, and an acidification step was included to separate degradation products (phaeophytin) from Chl *a* [100]. Data are expressed as mg Chl *a* per gram of sediment. Organic matter content was determined by drying the sediment at 60 °C for 48 h and then combusting it at 400°C for 5.5 h, with OM expressed as percent dry weight lost on ignition. For sediment grain size, samples were homogenised and then digested in ~ 9 % hydrogen peroxide until frothing ceased. Samples were then wet sieved through 2000 μm, 500 μm, 250 μm and 63 μm mesh sieves. Pipette analysis [101] was used to separate the <63 μm fraction into >3.9 μm

Table 7
Summary results of the GAM analyses assessing Functional Redundancy. Chl a: Chlorophyll a; Mud: Mud content in sediment; OM: Organic content in sediment; SST: Sea Surface Temperature; SOI: Southern Oscillation Index, Significant interactions are highlighted in bold.

Functional Redundancy				
	edf	**Ref.df**	**F**	**P-value**
a) HL				
s(Year)	3.922	4.924	8.824	**0.000002**
s(SOI)	1.452	1.782	0.327	0.775019
s(SST)	1	1	16.514	**0.000125**
s(Chla)	1	1	3.31	0.073144
s(Mud)	1	1	5.842	**0.018261**
s(OM)	1	1	0.463	0.498493
		R^2=0.62	Dev. Exp. = 67.23 %	
b) CB				
s(Year)	1	1	16.392	**0.000206**
s(SOI)	1.263	1.483	0.099	0.793413
s(SST)	1	1	11.25	**0.001647**
s(Chla)	1	1	1.116	0.296608
s(Mud)	3.089	3.83	3.474	**0.020809**
s(OM)	1	1	0.645	0.426314
		R^2=0.31	Dev. Exp. = 42.6 %	
c) MH				
s(Year)	4.732	5.805	3.302	**0.00647**
s(SOI)	4.301	5.303	1.257	0.27202
s(SST)	1.002	1.004	0.148	0.70232
s(Chla)	1	1	0.778	0.38077
s(Mud)	1	1	7.488	**0.00782**
s(OM)	1	1	0.449	0.50486
		R^2=0.36	Dev. Exp. = 46 %	
d) DC				
s(Year)	1	1	4.992	**0.0292**
s(SOI)	1	1	0.069	0.7935
s(SST)	2.435	2.976	1.561	0.2056
s(Chla)	1	1	0.146	0.7036
s(Mud)	1	1	0.022	0.8834
s(OM)	1	1	0.022	0.8815
		R^2=0.106	Dev. Exp. = 20.5 %	
e) TK				
s(Year)	1	1	0.018	0.89497
s(SOI)	1	1	1.637	0.204464
s(SST)	1	1	14.141	**0.000324**
s(Chla)	1	1	0	0.99843
s(Mud)	1	1	0.527	0.470142
s(OM)	1	1	0.018	0.892277
		R^2=0.13	Dev. Exp. = 19.4 %	
d) JB				
s(Year)	3.145	3.929	19.574	**0.000002**
s(SOI)	2.194	2.775	1.165	0.38
s(SST)	1	1	0.002	0.962
s(Chla)	2.608	3.284	1.657	0.172
s(Mud)	1	1	0.315	0.577
s(OM)	1	1	0.591	0.445
		R^2=0.54	Dev. Exp. = 60.2 %	

and ≤3.9 μm particles. All fractions were dried at 60°C until they maintained a constant weight (based on weights at ~ 40 h and 48 h). Percentage dry weights, relative to total subsample weight of gravel/-shell hash (>2000 μm), coarse sand (500–2000 μm), medium sand (250–500 μm), fine sand (62.5–250 μm), silt (3.9–62.5 μm) and clay (≤3.9 μm) were calculated. Mud was the sum of the silt and clay fractions.

Monthly Southern Oscillation Index (SOI) values were obtained from the National Oceanographic and Atmospheric Administration (NOAA) website (https://www.cpc.ncep.noaa.gov). We assumed all sites in the estuary were exposed to the general climate pattern at the same time, the same SOI time-series data were applied to all six sites within Mahurangi Harbour (i.e., SOI values did not differ at the scale of sites within a harbour). Monthly mean Sea Surface Temperature (SST) values for Mahurangi Harbour were generated from satellite imagery (The Copernicus Climate Change Service - https://climate.copernicus.eu/) by extracting point-values from the grid-cell (4 km resolution) across Mahurangi Harbour in New Zealand. Like SOI, due to the scale of the Copernicus data (4 km), the same SST values were assigned to all sampling sites within the Harbour. Mean SST was used as an ecologically relevant indicator of background thermal variability, as it reflects the long-term regional warming trend influencing estuarine systems. While short-term temperature extremes and tidal exposure can strongly affect intertidal organisms, mean SST integrates broader oceanographic that shape baseline environmental conditions over decadal timescales.

2.3. Data analysis

All the statistical analyses and derived plots were created using R software [102]. Functional metrics were calculated using the package 'FD' [103] based on macrobenthic abundance (see summary details in Table 1) and the selection of a suite of six functional traits and 27 traits modalities. The selected functional traits describe behavioural, morphological, and physiological attributes of the identified macroinvertebrate organisms (Table S2), and constitute effects traits that are directly and indirectly linked to ecosystem processes and functions underpinning ecological redundancy and resilience (58,82,104]. Trait information was retrieved from The New Zealand Trait Database for shallow-water marine benthic invertebrates (NZTD) [105]. The NZTD utilises a fuzzy coding procedure, scoring each taxon from 0 to 1, with 0 being no affinity and 1 being high affinity to a trait (for details see [105]). We followed the SAMT [106] and NZTD [105] guidelines for allocating the trait information to each taxon, and when trait information of a particular taxon was missing, trait information from the closest phylogenetic taxon was used (see details in Table S3). A combination of five functional metrics was used as a proxy of Functional Diversity, each highlighting different components of the biodiversity [72,77,78]. The five metrics were: (i) Functional Richness (FRic), which provides the amount of functional space occupied by a community, i.e., the quantity of traits that are expressed in a habitat [77,82]; (ii) Functional Evenness (FEve), which describes how consistently the taxa abundance is distributed across the expressed traits inside the functional space [77]; (iii) Functional Divergence (FDiv), which measures the degree the abundance of a community is distributed toward the extremities of the occupied functional trait space [71,77]; (iv) Functional Dispersion (FDis), estimated as the mean abundance of the community in the trait space [76]; and (v) Functional Redundancy (FR), the ratio between FD and Shannon diversity index–H' (FD/H'), which was used for investigating the expression of traits that were less common in the available functional space to assess trait expression stability of ecosystem functioning in the studied estuary. H' data were calculated from the raw macrobenthic data. Note that when the ratio of FD: H' decreases, FR increases and vice versa [82,107].

Collinearity among environmental drivers was assessed using Spearman correlation coefficients (Fig. S1) using the package "corrplot" [108] and Variance Inflation Factor (VIF) statistics using the package "car" [109] (Table S1). There was little to no collinearity in the environmental drivers used (e.g., VIF <3), thus all environmental drivers were able to be used together in subsequent analyses. Generalised Additive Models (GAMs) were employed to evaluate the temporal trends in the environmental variables Chal *a*, OM, Mud content, SOI, and SST using the "mgcv" [110,111] and "ggplot2" [112] packages in R software.

To evaluate the relationship between each macrobenthic functional metric (i.e., FRic, FEve, FDiv, FDis, and FR) and the five environmental drivers (Chl *a*, OM, Mud, SST, SOI), plus variation over time (Years), we employed Generalised Additive Models (GAMs) coded using the "mgcv" [110,111] and "ggplot2" [112] packages. Individual GAMs (i.e., one per site), were constructed using the residual maximum likelihood method (REML) and formula "$y \sim s(x_1) + s(x_n) + \varepsilon$" to best fit the observations [111]. Backward, forward, or stepwise techniques to determine final models were not used, rather we used all six potential environmental predictors in each GAM. Despite potential overfitting and collinearity,

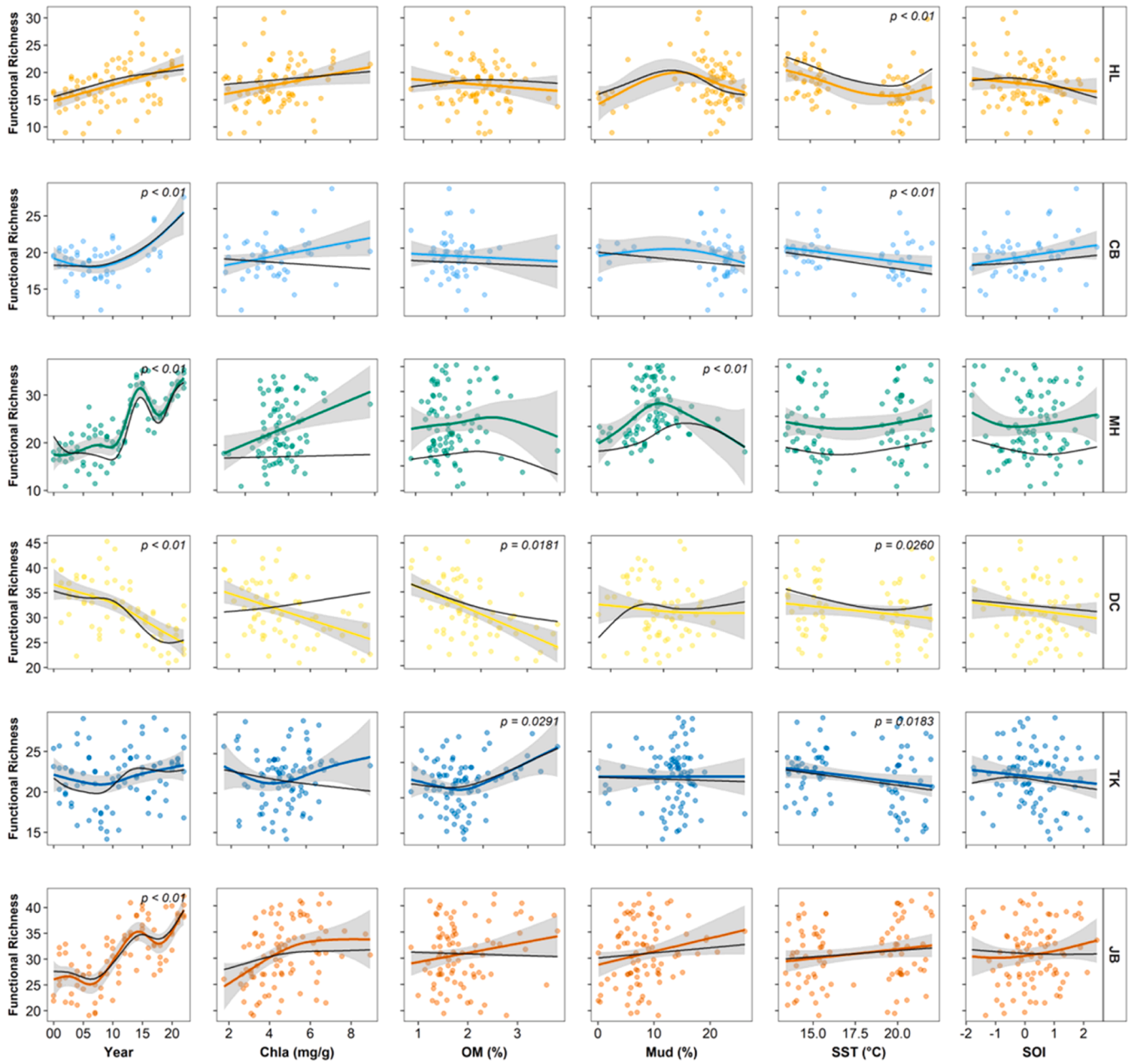

Fig. 4. Summary results of GAMs by site in Mahurangi Harbour. Partial residual plots indicating the direction of relationships between Functional Richness and temporal and environmental variables. Black solid lines show predicted values; coloured solid lines show the locally estimated smoothing trends; grey shading shows the 95 % confidence, and coloured solid points show the residual values. Significant interactions are showed as noted p values.

our aim was to evaluate responses using the same set of explanatory variables in all cases for comparative purposes. We were able to rule out collinearity by checking that variance inflation factors were always <3, and model evaluation did not show any overfitting. Partial regression residual plots, as a mean of GAM summary visualisation, were used to evaluate effects of individual predictors on responses while accounting for the effects of the other five variables using the R packages "gratia" [113] and "sjPlot" [114].

3. Results

3.1. Patterns of environmental drivers

The environmental drivers analysed varied over time and across sites (Figs. 2, 3). GAMs indicated upward trends over time in Chl *a* (~4 mg/g on average) at all sites, with the trends significant at HL, CB, and JB (Table 2, Fig. 2a). The Chl *a* record showed three periods, each roughly ten years apart, with slightly elevated values (2000–2002, 2010–2012, and 2020–2022). Chl *a* was highest at sites HL and CB in the inner estuary, while Chl *a* was lowest at site JB, located closest to the mouth (Fig. 2a). Organic matter (OM) content also varied by site over time (Table 2, Fig. 2b). The highest OM content was observed at site HL in the inner estuary, and the lowest OM was recorded at site DC, the furthest towards the mouth (Fig. 2b). GAMs showed OM to significantly increase over time at all sites except at CB site (Table 2, Fig. 2b). Sediment mud content (Mud) was highest at site HL in the upper estuary and lowest at site JB near the mouth (Fig. 2c). Sediment mud content increased over time at all sites, with significant increases at three of the six sites (Table 2, Fig. 2c).

The expected seasonal cyclicity in Sea Surface Temperature (SST)

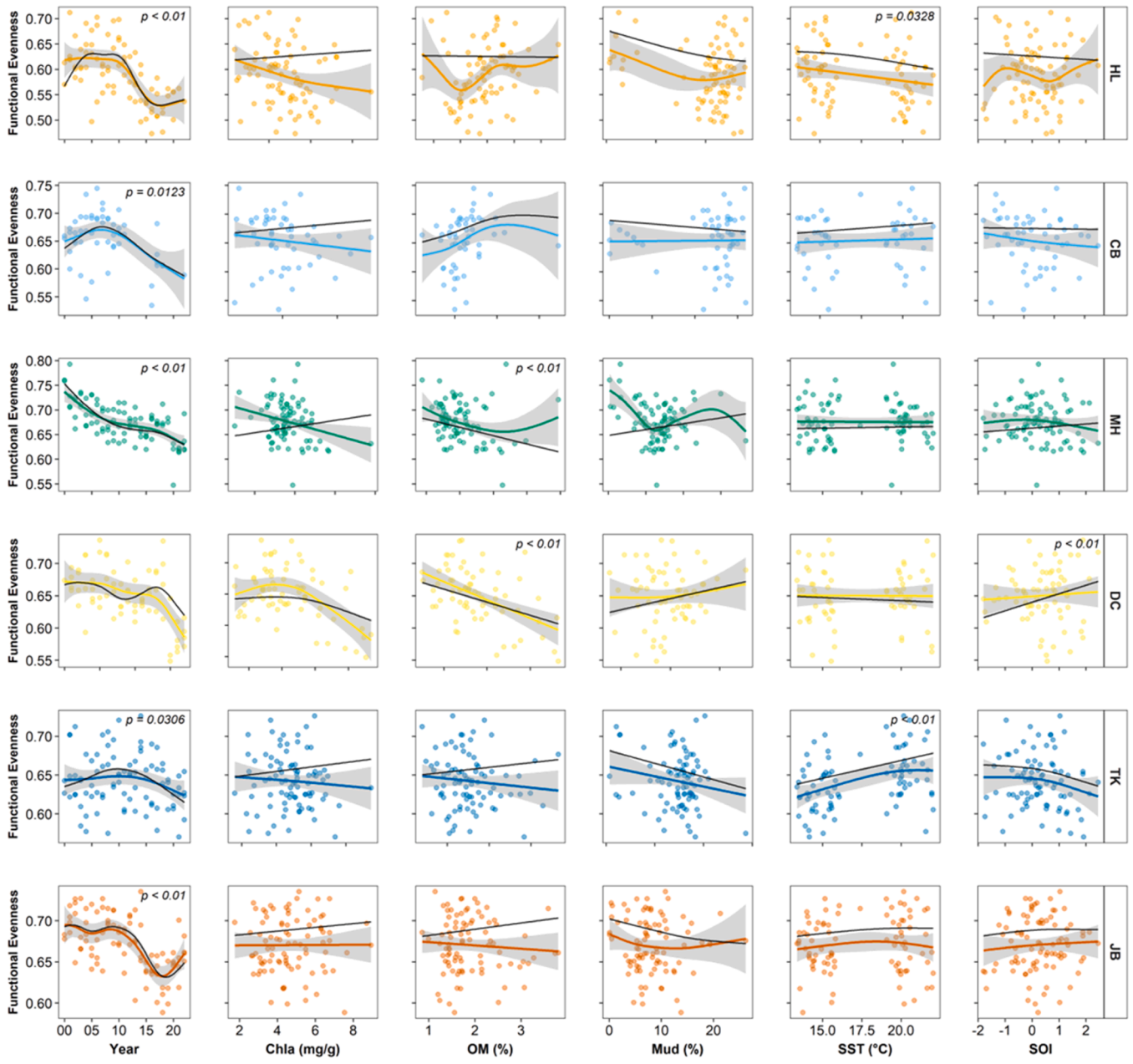

Fig. 5. Summary results of GAMs by site in Mahurangi Harbour. Partial residual plots indicating the direction of relationships between Functional Evenness and temporal and environmental variables. Black solid lines show predicted values; coloured solid lines show the locally estimated smoothing trends; grey shading shows the 95 % confidence intervals, and coloured solid points show the residual values. Significant interactions are showed as noted p values.

was observed, with warmer SST in summer and colder SST in winter every year (Fig. S2). The SST time series revealed an approximately 1°C increase in average SST in the harbour between 2000 and 2022 (Table 2, Figs. 3a, S2). The increase in SST over time was statistically significant for 'autumn only' data (Table 2, Fig. 3a) and 'one-year running mean' SST data (Fig. S2). Seasonal variability (~15° to 22°C) overwhelmed the smaller long-term increasing trend (~1°C) when raw SST values were analysed without smoothing or seasonal grouping. The Southern Oscillation Index (SOI) exhibited alternating periods of El Niño and La Niña conditions (Fig. 3b). In New Zealand, El Niño generally corresponds to warmer dryer weather, with La Niña corresponding to colder and wetter weather. Despite being an oscillating phenomenon, the GAM for the 22-year period analysed revealed increasing SOI over time (i.e., relatively more of the warmer El Niño conditions in the latter part of the time-series; Table 2, Fig. 3b).

3.2. *Drivers of estuarine macrobenthic functional metrics*

GAMs revealed the influences of the six environmental predictors on the five functional metrics (Tables 3–7, Figs. 4–8). In total, thirty GAMS were run (6 sites x 5 functional metrics), each with the same set of six predictors (Year, Chla, mud, OM, SST, and SOI). Each predictor was significant in at least three GAMs, except Chl *a* which was not significant in any model. The temporal variable (Year) and SST were significant the most often (17 and 12 models each, respectively), followed by Mud (7 models). SOI was only significant in three GAMs (Figs. 4–8). Across sites, significant effects of temporal and environmental drivers on functional metrics were observed most often at DC (11 times), followed by MH (9 instances), and HL, CB, and JB sires with 8 instances each.

Overall, Functional Richness (FRic) was significantly influenced by Year, OM, Mud, and SST drivers (Table 3, Fig. 4). Multiple responses of FRic to temporal and environmental drivers were identified. For

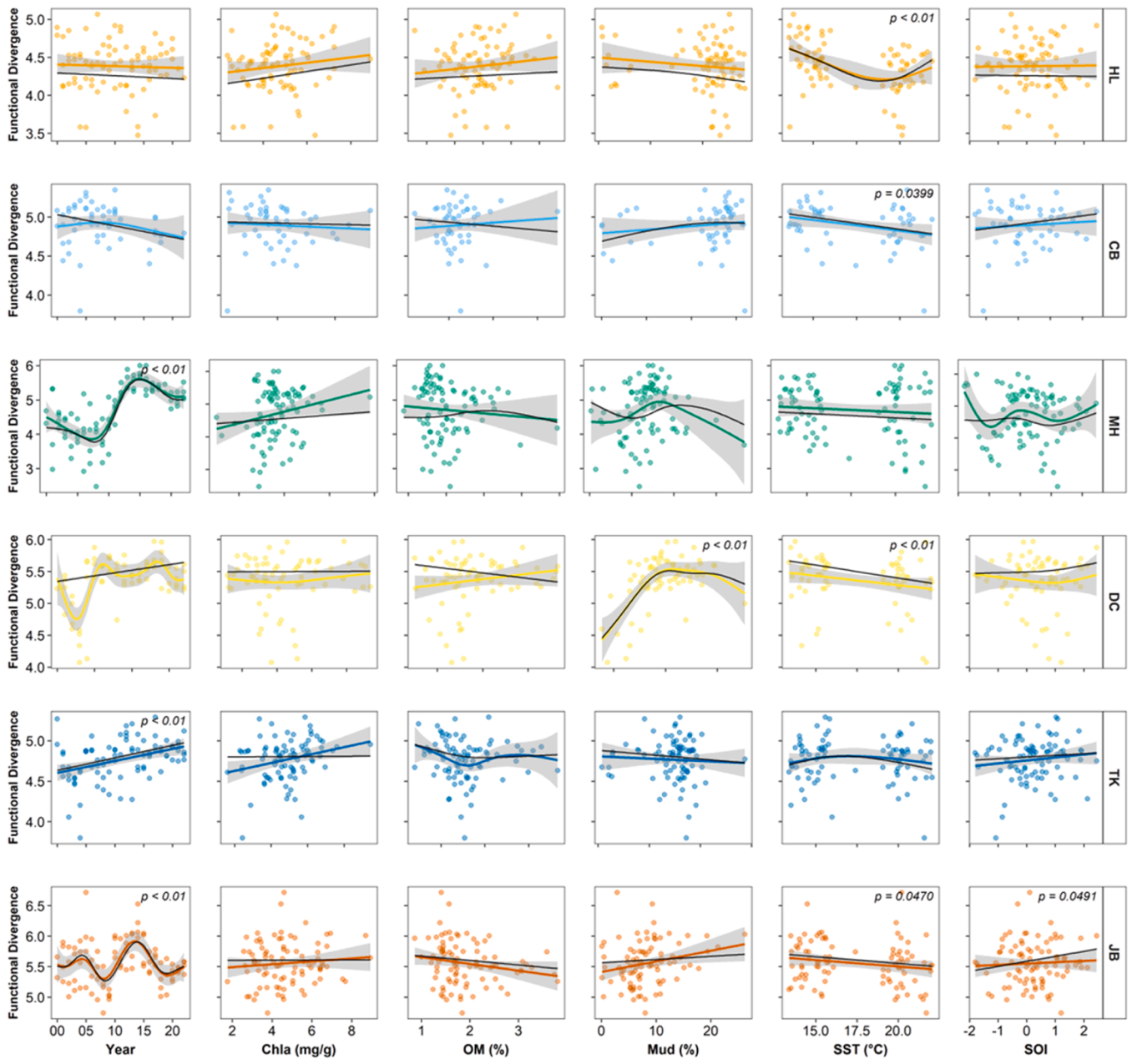

Fig. 6. Summary results of GAMs by site in Mahurangi Harbour. Partial residual plots indicating the direction of relationships between Functional Divergence and temporal and environmental variables. Black solid lines show predicted values; coloured solid lines show the locally estimated smoothing trends; grey shading shows the 95 % confidence intervals, and coloured solid points show the residual values. Significant interactions are showed as noted p values.

example, FRic tended to increase over time in five of the six sites analysed (Fig. 4). FRic significantly decreased when Mud content in sediment was above 20 % at MH (Fig. 4). Increasing OM also contributed to decreased FRic at site DC, but increased FRic at TK. FRic at sites HL, CB, DC, and TK decreased with increasing SST (Fig. 4).

Functional Evenness (FEve) was significantly influenced by Year, OM, SST, and SOI at least once at each of the study sites (Table 4, Fig. 5). FEve significantly decreased over time (Fig. 5). FEve significantly decreased with increasing OM at sites MH and DC, and increasing SST at site HL. In contrast, FEve values increased with increasing SST at site TK and increasing SOI at site DC (Fig. 5). Functional Divergence (FDiv) was influenced by most of the temporal and environmental drivers except Chl *a* and OM (Table 5, Fig. 6). Similar to FRic, FDis tended to increase over time (Fig. 6). Mixed responses were also identified, for example, FDiv significantly increased with increasing Mud at DC; decreased with increasing SST at sites HL, CB, DC, and JB; and increased with increasing SOI at site JB.(Fig. 6).

Functional Dispersion (FDis) followed a similar pattern to FDiv, responding to the influence of Year, Mud, SST, and SOI, while influences of Chl *a* and OM were not detected (Table 6, Fig. 7). FDis was affected by changes in temporal and environmental variables at five of the six sites, with some mixed responses identified. For example, FDis significantly increased over time at sites DC and JB, but tended to decrease at sites HL, CB, and MH. FDis also showed decreasing trends with increasing Mud at site MH and DC (Fig. 7). Yet, a relatively consistent response to SST was identified, for example FDis significantly decreased with increasing SST at JB (Fig. 7). Functional Redundancy (FR) showed a similar pattern to FDiv and FDis, with Year, Mud, and SST influencing FR (Table 7, Fig. 8). FR tended to significantly decrease over time at sites HL, CB, MH, and JB, but increased over time at DC (Fig. 8). The influence of Mud on FR was consistent; FR significantly decreased with increasing Mud at HL, CB, and MH, and increased with increasing SST at

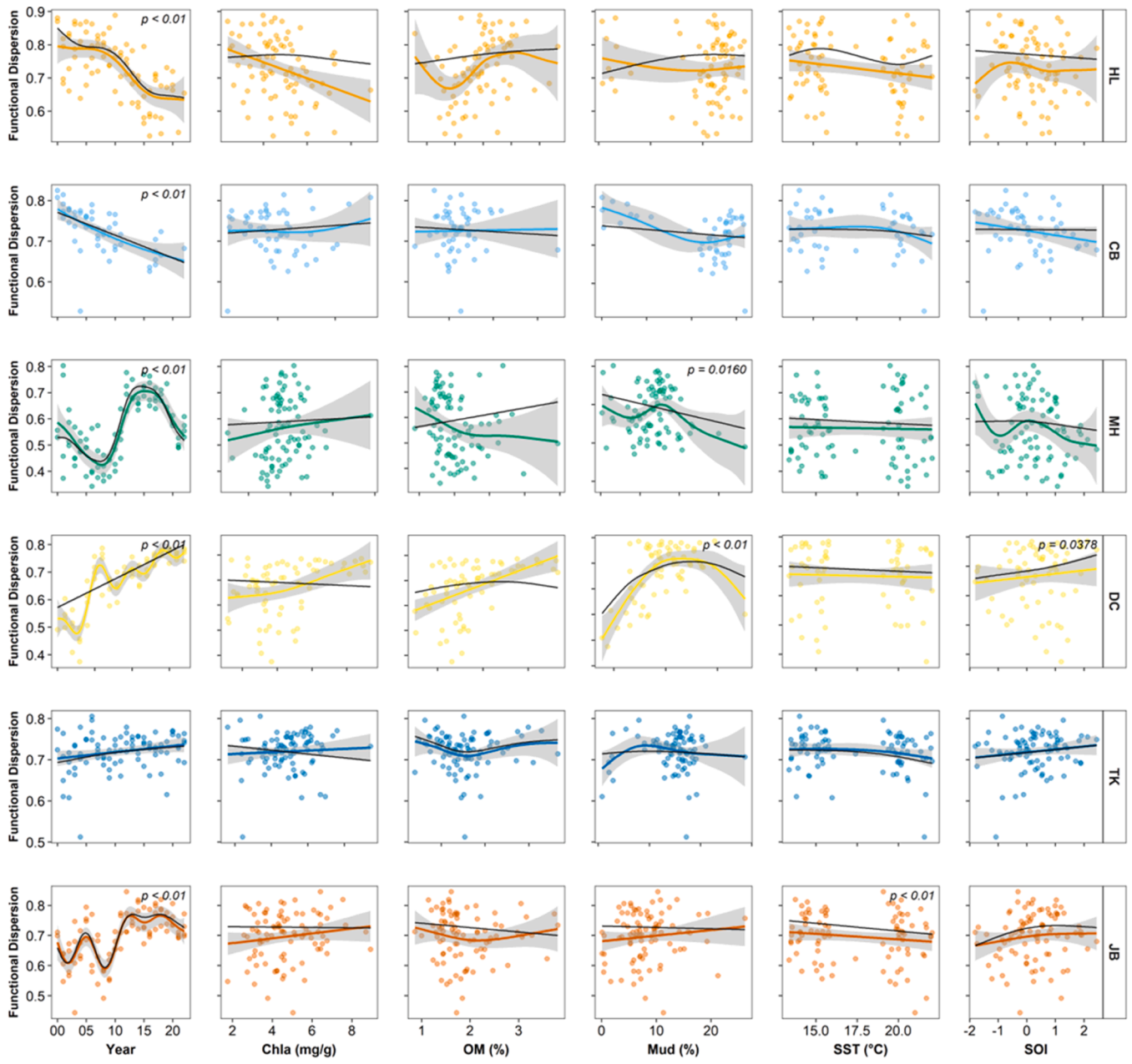

Fig. 7. Summary results of GAMs by site in Mahurangi Harbour. Partial residual plots indicating the direction of relationships between Functional Dispersion and temporal and environmental variables. Black solid lines show predicted values; coloured solid lines show the locally estimated smoothing trends; grey shading shows the 95 % confidence intervals, and coloured solid points show the residual values. Significant interactions are showed as noted p values.

sites HL, CB and TK (Fig. 8).

4. Discussion

Climate change is affecting estuarine ecosystems in multiple ways, generating a mix of direct and indirect influences, some that may be stressors and some that may positively impact estuarine biota and functions. Our exploration of estuarine environmental variables over a 22-year period at six sites in Mahurangi Harbour highlighted three general trends: increasing sea surface temperatures (satellite-derived SST), increasing sediment food supply (Chl *a* and OM), and increasing bed sediment muddiness (percent mud content). The SST trend is consistent with the relative rapid increase in planetary temperatures observed over the last 20 years [5,8], and reports of increased marine heat wave activity in New Zealand during the same period [115–117]. Yet there is considerable local scale variation in sea surface temperature and warming trends may not be detectable in all estuaries in New Zealand [118–121].

We interpret the increasing trends in Chl *a* observed at several sites—an indicator of increased abundance of microphytobenthos—as a positive indirect effect of long-term warming, which is consistent with previous studies [52,122–124]. For macroinvertebrate communities, the higher sediment Chl *a* content is likely to be indicative of higher primary food supply [125,126], which would contribute positively to macrofauna populations via enhanced fitness and reproductive output, as observed in a previous study in NZ showing increasing macrobenthic patterns (i.e. abundance, richness) over time influenced by Chl *a* concentrations [59].

During the past 20 years, catchments surrounding Mahurangi Harbour have been rapidly transitioning from pastoral to suburban. Changes in land-use and concomitant erosion of sediments from catchments have been cited as causes of increased terrigenous sediment

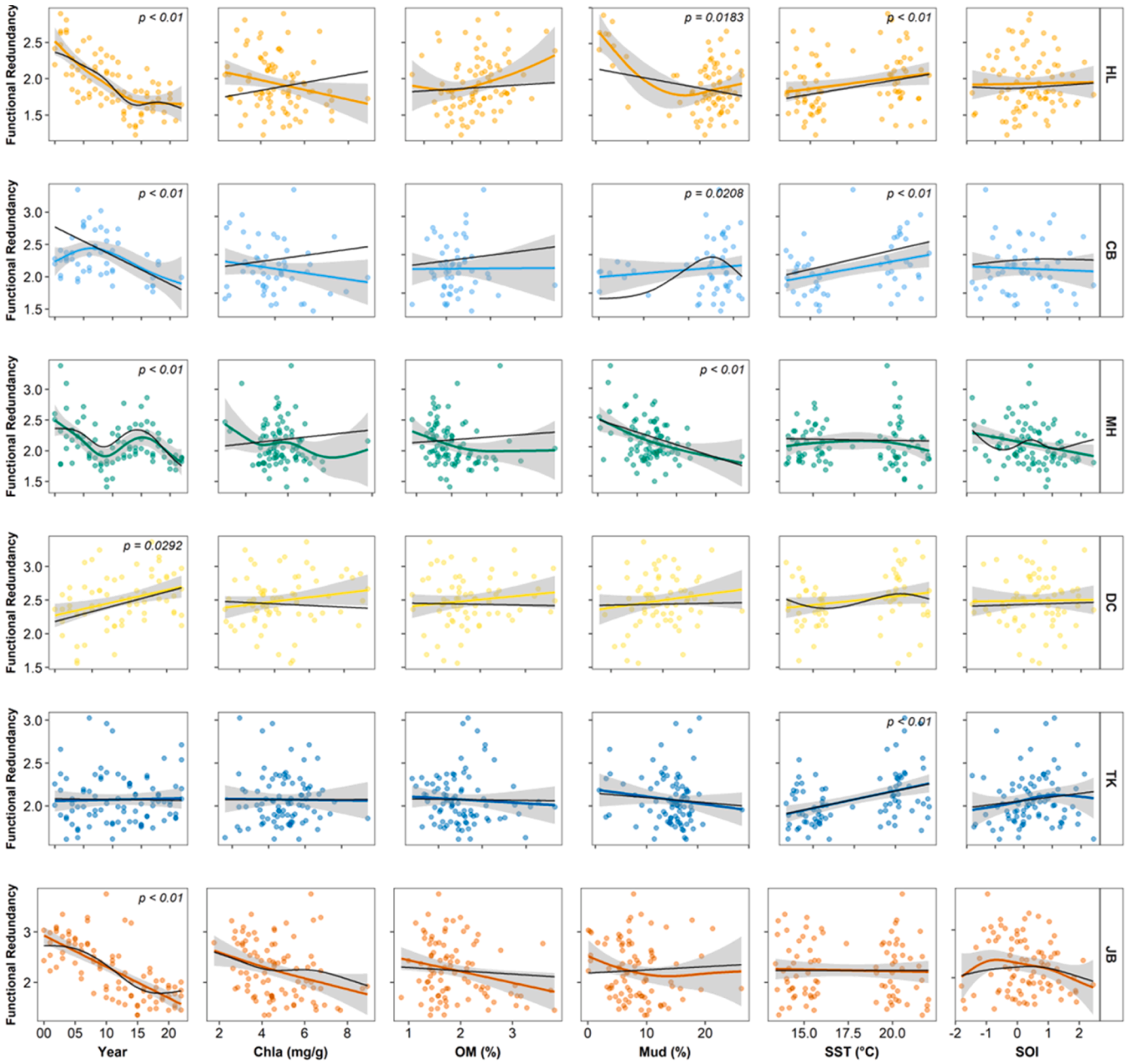

Fig. 8. Summary results of GAMs by site in Mahurangi Harbour. Partial residual plots indicating the direction of relationships between Fucntional Redundancy and temporal and environmental variables. Black solid lines show predicted values; coloured solid lines show the locally estimated smoothing trends; grey shading shows the 95 % confidence intervals, and coloured solid points show the residual values. Significant interactions are showed as noted p values.

loading to this estuary [41,42,92]. Furthermore, the increase in frequency and intensity of climatic events, such as cyclones, storms, and in general increased precipitation, can modify river discharge and water flow, resulting in increased sediment deposition and alteration of sediment characteristics in estuarine ecosystems [27,127,128]. Trends of increasing bed sediment muddiness observed at sites throughout the estuary from 2000–2022 are consistent with increased terrigenous sediment loading, and mud is widely viewed as a major stressor in the system. Accordingly, macrobenthic abundance and richness decreased at some sites in Mahurangi Harbour with increasing sediment muddiness [59,129]. We cannot determine whether increased storm frequency and intensity has already accelerated the increase in muddiness of estuarine habitats within Mahurangi Harbour, but a recent study across two estuaries in New Zealand showed increases in estuarine muddiness after a cyclone with effects on the macroinvertebrate communities [128]. Thus, we consider increasing sediment mud content to be an indirect deleterious climate-related driver of macrobenthic functional redundancy and resilience.

A primary motivation for the study was to determine the simultaneous effects of multiple climate-related drivers on estuarine macrobenthic functional redundancy and resilience. We had high-quality time-series data to work with, and an ability to calculate Functional Diversity statistics using a recently published traits database [105]. Previous investigations have focused on responses of macrobenthic abundance, taxonomic richness and community structure to individual and combined environmental drivers (e.g., [59,129–131]). Here, however, we focused on investigating responses of five functional metrics to multiple environmental drivers to gain insights into macrobenthic functional change as CO_2 emissions and temperatures continue to rise.

Results of our study showed that most of the macrobenthic functional

metrics (FRic, FDis, FDiv, FR) assessed increased over time, except FEve, which decreased over time. Our findings provided mixed support for our hypotheses. We predicted positive effects of sediment chlorophyll *a* on functional metrics, yet we did not find significative evidence supporting this prediction. Despite the lack of statistically significance from or models, general trends showed increases in functional metrics with increasing Chl *a*. These patterns likely reflect changes in food availability in the system, with increased macrobenthic functionality (i.e., FRic, FEve, FDiv, FDis, FR) as response to greater amounts of food [59, 132].

Evidence of the negative effects of organic matter and mud content in sediment on functional metrics was mixed. OM showed a significant negative effect on FRic and FEve at the MH and DC sites but a positive effect on FRic at TK. OM is also related to macrobenthic food supply consumed primarily by deposit feeders and grazers [87,125,132,133]. Positive effects on FRic (increased FRic with increasing OM) could be explained as a response to increased food availability that can occur especially when OM content is present at low to moderate levels [132, 134], while negative effects of OM on FRic and FEve could be the response of excessive organic matter content (>5 %), promoting the onset of eutrophication symptoms [42,130,132] that negatively impact macrobenthic functioning.

Mud had a significant negative effect on FRic, FDiv, FDis, and FR at the inner harbour sites HL, CB, MH, and DC. Macrobenthic functional metrics declined with increases in sediment mud content above ~10 % at most of the sites across Mahurangi harbour . This is consistent with prior studies in New Zealand suggesting reduced macrobenthic abundance and richness beyond certain thresholds in bed sediment muddiness [41,42,59,129,130]. FR was the functional metric most negatively affected by Mud (three of six sites), suggesting reduced resilience at these sites due to the elevated content of mud in sediment which is consistent with previous literature [42,135,136].

We also hypothesised positive effects of SST on macrobenthic functional metrics, but our findings provided mixed support for this prediction as well . SST had negative effects on all functional metrics, FRic and FDiv at four of the six sites, FR at three of six sites, and FEve and FDis at one site, while the only positive effect was identified on FEve at one site. These findings consistently suggest a negative effect of increasing SST on resilience. Increases in SST could affect the morphology, life history, abundance, and distribution of benthic organisms [131, 137–139] that are less adapted to the warming temperatures, which could explain the negative effects of SST identified in our study. Yet, the net result of higher FRic over time could stem from increasing expression of macrobenthic functional traits adapted for increasing temperatures, i.e., increased abundance, diversity and number of taxa, which aligns with findings in previous studies (e.g., [59,83,140]). In contrast, the general trend of decreasing FD/H' over time, reflected as increasing FR, could be related to SST causing macrobenthic communities to express a wide range of functional traits that are resistant or better adapted to global warming

The position of sites in the estuary also appeared to influence results. Higher FRic was found in sites located in the outer section of the estuary (near the mouth), while lower FRic was identified in sites in the inner part of the estuary. The main river tributary delivering sediment to Mahurangi Harbour enters in the innermost section, and sites in the inner harbour are generally much muddier than those near the mouth. Site dependent results have been previously reported in other marine and estuarine systems, which were attributed to specific environmental conditions and benthic habitat characteristics such as organic matter content in sediment, and sediment particle size distribution [80,82,90, 131,141].

Functional Evenness (FEve), i.e., the consistency of the taxa abundance and traits expressed in a functional space, showed a decreasing pattern in all the studied sites over time, which suggested high variability in macrofauna abundance and their functional traits over time [71,72,77]. FEve did not vary temporally but differed between inner and outer harbour sites. In contrast, Functional Divergence (FDiv), i.e., the abundance outliers in a functional space, increased over time at half of the studied sites. Within-site variability in FDiv was less evident in recent years, suggesting a homogenisation in abundance and traits expressed over time [71,72,77]. The mean distance between species within a community in a functional space, i.e., Functional Dispersion (FDis) was mixed across sites and showed a pattern of functional homogenisation over time, suggesting that the species and trait expression became more similar within communities over time [76].

The ratio of FD/H' decreased over time at almost all of the study sites (five of six), indicating a trend of increasing Functional Redundancy (FR). High FR indicates that multiple taxa are occupying the available functional trait space, and that the diversity of functional traits is higher. It has been suggested that the greater the number of taxa and functional traits expressed in an ecosystem, the greater probability of taxa and traits to persist and maintain ecosystem functioning in the face of individual species losses [82,107,142,143]. Thus, the macrobenthic functioning present in Mahurangi Harbour may be slightly more resilient and more likely to maintain ecosystem functioning now, relative to the early 2000s, with the net overall increase of FR over time driven predominantly by the influence of increasing tidal flat food supply (Chl *a*, OM) overriding the negative effects of increasing Mud and SST.

Although our study advances understanding of long-term changes in estuarine macrobenthic functionality, it is important to highlight the omission of certain broad-scale climatic drivers. Climatic variables such as air temperature, pH, sea level rise, and precipitation could be also driving the long-term macroinvertebrate functional patterns observed, yet we were not able to include these climatic drivers due to the absence of consistent, high-resolution data spanning the full temporal and spatial extent of our study. Instead, we focused on five environmental variables (e.g., sedimentary, climatological, oceanic) as proxies of climatic variability that reportedly influence macroinvertebrate communities and ecosystems functions. However, these parameters capture only part of the environmental complexity associated with climate change. Furthermore, the outcomes presented in our study showed the long-term patterns in estuarine macrobenthic functional metrics, and detailed individual traits or species-specific contributions and dynamics over time were not fully explored. We suggest that future research could incorporate a wider range of climatic variables combined with high-resolution monitoring of individual functional traits will be crucial to better understand how temporal variation in macroinvertebrate functionality contributes to ecosystem functioning, redundancy, and resilience in response to climate change.

5. Conclusion

Our investigation assessing temporal and environmental relationships with macrobenthic functional metrics over 22 years suggested trends of increasing SST and sediment muddiness, which influenced the macrobenthic functional diversity in the studied estuary. Global warming, extreme weather, and heat spikes exacerbate desiccation and thermal stress to intertidal macroinvertebrates which are likely to be deleterious in the short-term. However, our data provides evidence that some macrobenthic organisms, based on our analysis of functional metrics, may be increasingly resilient and adaptable, rather than increasingly depauperate and functionally impacted, as sea surface temperatures rise.

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CRediT authorship contribution statement

Orlando Lam-Gordillo: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Andrew M. Lohrer:** Writing – review & editing, Writing – original draft, Validation, Supervision, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

No potential conflict of interest was reported by the authors.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecochg.2025.100100.

Data availability

All the data used is presented in the article and supplementary materials.

References

[1] Copernicus, Copernicus: 2023 is the hottest year on record, with global temperature close to the 1.5°C limit. Copernicus Climate Change Service, Copernicus Atmosphere Monitoring Service, 2024.
[2] NASA. 2024. Five factors to explain the record heat in 2023. NASA Earth Observatory.
[3] C. Wong, Earth just had its hottest year on record — Climate change is to blame, Nature 623 (2023) 674–675.
[4] B. Bronselaer, L. Zanna, Heat and carbon coupling reveals ocean warming due to circulation changes, Nature 584 (2020) 227–233.
[5] W. Deng, Ocean warming and warning, Nat. Clim. Chang. 14 (2024) 118–119.
[6] M.F. Huguenin, R.M. Holmes, M.H. England, Drivers and distribution of global ocean heat uptake over the last half century, Nat. Commun. 13 (2022) 4921.
[7] Z. Li, M.H. England, S. Groeskamp, Recent acceleration in global ocean heat accumulation by mode and intermediate waters, Nat. Commun. 14 (2023) 6888.
[8] H.S. Findlay, C. Turley, Chapter 13 - ocean acidification and climate change, in: T.M. Letcher (Ed.), Climate Change (Third Edition), Elsevier, 2021, pp. 251–279.
[9] C. Mellin, S. Brown, N. Cantin, E. Klein-Salas, D. Mouillot, S.F. Heron, D. A. Fordham, Cumulative risk of future bleaching for the world's coral reefs, Sci. Adv. 10 (2024) eadn9660.
[10] A. Virgen-Urcelay, S.D. Donner, Increase in the extent of mass coral bleaching over the past half-century, based on an updated global database, PLoS One 18 (2023) e0281719.
[11] J. Assis, E. Fragkopoulou, L. Gouvêa, M.B. Araújo, E.A. Serrão, Kelp forest diversity under projected end-of-century climate change, Divers. Distrib. 30 (2024) e13837.
[12] K.A. Krumhansl, C.M. Brooks, J.B. Lowen, J.M. O'Brien, M.C. Wong, C. DiBacco, Loss, resilience and recovery of kelp forests in a region of rapid ocean warming, Ann. Bot. 133 (2023) 73–92.
[13] L.S. Wright, A. Pessarrodona, A. Foggo, Climate-driven shifts in kelp forest composition reduce carbon sequestration potential, Glob. Chang. Biol. 28 (2022) 5514–5531.
[14] E.J. Chapman, C.J. Byron, R. Lasley-Rasher, C. Lipsky, J.R. Stevens, R. Peters, Effects of climate change on coastal ecosystem food webs: implications for aquaculture, Mar. Environ. Res. 162 (2020) 105103.
[15] D.G.E. Gomes, J.J. Ruzicka, L.G. Crozier, D.D. Huff, R.D. Brodeur, J.D. Stewart, Marine heatwaves disrupt ecosystem structure and function via altered food webs and energy flux, Nat. Commun. 15 (2024) 1988.
[16] R.H. Heleno, W.J. Ripple, A. Traveset, Scientists' warning on endangered food webs, Web Ecol. 20 (2020) 1–10.
[17] J.P. Queirós, R. Borras-Chavez, N. Friscourt, J. Groß, C.B. Lewis, G. Mergard, K. O'Brien, Southern ocean food-webs and climate change: a short review and future directions, PLOS Clim. 3 (2024) e0000358.
[18] S.E. Campana, R.B. Stefánsdóttir, K. Jakobsdóttir, J. Sólmundsson, Shifting fish distributions in warming sub-Arctic oceans, Sci. Rep. 10 (2020) 16448.
[19] M. Huang, Y. Chen, W. Zhou, F. Wei, Assessing the response of marine fish communities to climate change and fishing, Conserv. Biol. 38 (6) (2024) e14291.
[20] V.W.Y. Lam, E.H. Allison, J.D. Bell, J. Blythe, W.W.L. Cheung, T.L. Frölicher, M. A. Gasalla, U.R. Sumaila, Climate change, tropical fisheries and prospects for sustainable development, Nat. Rev. Earth Environ. 1 (2020) 440–454.
[21] D.J. McKenzie, B. Geffroy, A.P. Farrell, Effects of global warming on fishes and fisheries, J. Fish Biol. 98 (2021) 1489–1492.
[22] C.A. Brown, D. Sharp, T.C. Mochon Collura, Effect of climate change on water temperature and attainment of water temperature criteria in the Yaquina Estuary, Oregon (USA), Estuar. Coast. Shelf. Sci. 169 (2016) 136–146.
[23] E. Scanes, P.R. Scanes, P.M. Ross, Climate change rapidly warms and acidifies Australian estuaries, Nat. Commun. 11 (2020) 1803.
[24] S.F. Thrush, J.E. Hewitt, C. Pilditch, A. Norkko, Ecology of Coastal Marine Sediments: Form, Function, and Change in the Anthropocene, Oxford, 2021.
[25] S.M. Bashevkin, B. Mahardja, L.R. Brown, Warming in the upper San Francisco Estuary: patterns of water temperature change from five decades of data, Limnol. Oceanogr. 67 (2022) 1065–1080.
[26] P. Prum, L. Harris, J. Gardner, Widespread warming of Earth's estuaries, Limnol. Oceanogr. Lett. 9 (2024) 268–275.
[27] J.E. Cloern, P.C. Abreu, J. Carstensen, L. Chauvaud, R. Elmgren, J. Grall, Human activities and climate variability drive fast-paced change across the world's estuarine–coastal ecosystems, Glob. Change Biol. 22 (2016) 513–529.
[28] N.N. Rabalais, R.E. Turner, R.J. Díaz, D. Justić, Global change and eutrophication of coastal waters, ICES J. Mar. Sci. 66 (2009) 1528–1537.
[29] A. Villnäs, U. Janas, A.B. Josefson, H. Kendzierska, H. Nygård, J. Norkko, A. Norkko, Changes in macrofaunal biological traits across estuarine gradients: implications for the coastal nutrient filter, Mar. Ecol. Prog. Ser. 622 (2019) 31–48.
[30] C.A. Burge, C. Mark Eakin, C.S. Friedman, B. Froelich, P.K. Hershberger, E. E. Hofmann, L.E. Petes, K.C. Prager, E. Weil, B.L. Willis, Climate change influences on marine infectious diseases: implications for management and society, Ann. Rev. Mar. Sci. 6 (2014) 249–277.
[31] S.K. Moore, V.L. Trainer, N.J. Mantua, M.S. Parker, E.A. Laws, L.C. Backer, L. E. Fleming, Impacts of climate variability and future climate change on harmful algal blooms and human health. Environmental Health, Springer, 2008, pp. 1–12.
[32] Y. Costa, I. Martins, G.C. de Carvalho, F. Barros, Trends of sea-level rise effects on estuaries and estimates of future saline intrusion, Ocean. Coast. Manage 236 (2023) 106490.
[33] K.A. Erickson, J. West, M.A. Dance, T.M. Farmer, J.C. Ballenger, S.R. Midway, Changing climate associated with the range-wide decline of an estuarine finfish, Glob. Chang. Biol. 27 (2021) 2520–2536.
[34] D. Khojasteh, W. Glamore, V. Heimhuber, S. Felder, Sea level rise impacts on estuarine dynamics: a review, Sci. Total Environ. 780 (2021) 146470.
[35] D.G. Boyce, D.P. Tittensor, C. Garilao, S. Henson, K. Kaschner, K. Kesner-Reyes, A. Pigot, R.B. Reyes, G. Reygondeau, K.E. Schleit, N.L. Shackell, P. Sorongon-Yap, B. Worm, A climate risk index for marine life, Nat. Clim. Chang. 12 (2022) 854–862.
[36] S.A. Henson, C. Beaulieu, T. Ilyina, J.G. John, M. Long, R. Séférian, J. Tjiputra, J. L. Sarmiento, Rapid emergence of climate change in environmental drivers of marine ecosystems, Nat. Commun. 8 (2017) 14682.
[37] IPCC, Annex II: glossary [Möller, V., R. van Diemen, J.B.R. Matthews, in: C. Méndez, S. Semenov, J.S. Fuglestvedt, A. Reisinger (Eds.), (eds.)]. Pages 2897–2930 in H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, and B. Rama, editors. Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel On Climate Change, Cambridge, UK and New York, NY, USA, 2022.
[38] P.M. Chapman, Assessing and managing stressors in a changing marine environment, Mar. Pollut. Bull. 124 (2016) 587–590.
[39] T.C. Malone, A. Newton, The globalization of cultural eutrophication in the coastal ocean: causes and consequences, Front. Mar. Sci. 7 (2020).
[40] M. Meyneng, H. Lemonnier, R.Le Gendre, G. Plougoulen, F. Antypas, D. Ansquer, J. Serghine, S. Schmitt, R. Siano, Subtropical coastal microbiome variations due to massive river runoff after a cyclonic event, Environ. Microbiome 19 (2024) 10.
[41] E.J. Douglas, C.A. Pilditch, A.M. Lohrer, C. Savage, L.A. Schipper, S.F. Thrush, Sedimentary environment influences ecosystem response to nutrient enrichment, Estuaries Coasts 41 (2018) 1994–2008.
[42] A.M. Lohrer, S.F. Thrush, J.E. Hewitt, K. Berkenbusch, M. Ahrens, V.J. Cummings, Terrestrially derived sediment: response of marine macrobenthic communities to thin terrigenous deposits, Mar. Ecol. Prog. Ser. 307 (2004) 121–138.
[43] A.M. Lohrer, S.F. Thrush, C.J. Lundquist, K. Vopel, J.E. Hewitt, P.E. Nicholls, Deposition of terrigenous sediment on subtidal marine macrobenthos: response of two contrasting community types, Mar. Ecol. Prog. Ser. 307 (2006) 115–125.
[44] S. Mangan, K.R. Bryan, S.F. Thrush, R.V. Gladstone-Gallagher, A.M. Lohrer, C. A. Pilditch, Shady business: the darkening of estuaries constrains benthic ecosystem function, Mar. Ecol. Prog. Ser. 647 (2020) 33–48.
[45] S.F. Thrush, J.E. Hewitt, V.J. Cummings, J.I. Ellis, C. Hatton, A. Lohrer, A. Norkko, Muddy waters: elevating sediment input to coastal and estuarine habitats, Front. Ecol. Environ. 2 (2004) 299–306.
[46] F. Boscolo-Galazzo, K.A. Crichton, S. Barker, P.N. Pearson, Temperature dependency of metabolic rates in the upper ocean: a positive feedback to global climate change? Glob. Planet. Change 170 (2018) 201–212.

[47] A. Cossins, Temperature Biology of Animals, Springer Science & Business Media, 2012.
[48] K. Alter, J. Jacquemont, J. Claudet, M.E. Lattuca, M.E. Barrantes, S. Marras, P. H. Manríquez, C.P. González, D.A. Fernández, M.A. Peck, C. Cattano, M. Milazzo, F.C. Mark, P. Domenici, Hidden impacts of ocean warming and acidification on biological responses of marine animals revealed through meta-analysis, Nat. Commun. 15 (2024) 2885.
[49] M.E. Dillon, G. Wang, R.B. Huey, Global metabolic impacts of recent climate warming, Nature 467 (2010) 704–706.
[50] A. McGaughran, R. Laver, C. Fraser, Evolutionary responses to warming, Trends Ecol. Evol. 36 (2021) 591–600 (Amst.).
[51] M.J. Behrenfeld, R.T. O'Malley, E.S. Boss, T.K. Westberry, J.R. Graff, K.H. Halsey, A.J. Milligan, D.A. Siegel, M.B. Brown, Revaluating ocean warming impacts on global phytoplankton, Nat. Clim. Chang. 6 (2016) 323–330.
[52] K. Gao, J. Beardall, D.-P. Häder, J.M. Hall-Spencer, G. Gao, D.A. Hutchins, Effects of ocean acidification on marine photosynthetic organisms under the concurrent influences of warming, UV radiation, and deoxygenation, Front. Mar. Sci. 6 (2019) 322.
[53] M.P. Lesser, Climate change stressors cause metabolic depression in the blue mussel, Mytilus edulis, from the Gulf of Maine, Limnol. Oceanogr. 61 (2016) 1705–1717.
[54] F. Noisette, J. Richard, I. Le Fur, L.S. Peck, D. Davoult, S. Martin, Metabolic responses to temperature stress under elevated p CO2 in Crepidula fornicata, J. Molluscan Stud. 81 (2015) 238–246.
[55] J. Wang, L.-X. Ma, Y.-W. Dong, Coping with harsh heat environments: molecular adaptation of metabolic depression in the intertidal snail Echinolittorina radiata, Cell Stress Chaperones 28 (2023) 477–491.
[56] A. Borja, S.B. Bricker, D.M. Dauer, N.T. Demetriades, J.G. Ferreira, A.T. Forbes, P. Hutchings, X. Jia, R. Kenchington, J.C. Marques, C. Zhu, Overview of integrative tools and methods in assessing ecological integrity in estuarine and coastal systems worldwide, Mar. Pollut. Bull. 56 (2008) 1519–1537.
[57] A. Borja, J. Franco, V. Pérez, A marine biotic index to establish the ecological quality of soft-bottom benthos with European estuarine and coastal environments, Mar. Pollut. Bull. 40 (2000) 1100–1114.
[58] O. Lam-Gordillo, R. Baring, S. Dittmann, Ecosystem functioning and functional approaches on marine macrobenthic fauna: a research synthesis towards a global consensus, Ecol. Indic. 115 (2020) 106379.
[59] O. Lam-Gordillo, J.E. Hewitt, E.J. Douglas, B.D. Dudley, S.J. Holmes, S. Hailes, K. Carter, B. Greenfield, T. Drylie, A.M. Lohrer, Climatic, oceanic, freshwater, and local environmental drivers of New Zealand estuarine macroinvertebrates, Mar. Environ. Res. 197 (2024) 106472.
[60] J.R. Tweedley, R.M. Warwick, F.J. Valesini, M.E. Platell, I.C. Potter, The use of benthic macroinvertebrates to establish a benchmark for evaluating the environmental quality of microtidal, temperate southern hemisphere estuaries, Mar. Pollut. Bull. 64 (2012) 1210–1221.
[61] E. Kristensen, M. Delefosse, C.O. Quintana, M.R. Flindt, T. Valdemarsen, Influence of benthic macrofauna community shifts on ecosystem functioning in shallow estuaries, Front. Mar. Sci. 1 (2014) 41.
[62] E. Kristensen, G. Penha-Lopes, M. Delefosse, T. Valdemarsen, C.O. Quintana, G. T. Banta, What is bioturbation? The need for a precise definition for fauna in aquatic sciences, Mar. Ecol. Prog. Ser. 446 (2012) 285–302.
[63] L.T. Bach, J. Taucher, CO 2 effects on diatoms: a synthesis of more than a decade of ocean acidification experiments with natural communities, Ocean Sci. 15 (2019) 1159–1175.
[64] S. Dutkiewicz, J.J. Morris, M.J. Follows, J. Scott, O. Levitan, S.T. Dyhrman, I. Berman-Frank, Impact of ocean acidification on the structure of future phytoplankton communities, Nat. Clim. Chang. 5 (2015) 1002–1006.
[65] K. Gao, D.A. Campbell, Photophysiological responses of marine diatoms to elevated CO2 and decreased pH: a review, Funct. Plant Biol. 41 (2014) 449–459.
[66] J. Taucher, L.T. Bach, A.E.F. Prowe, T. Boxhammer, K. Kvale, U. Riebesell, Enhanced silica export in a future ocean triggers global diatom decline, Nature 605 (2022) 696–700.
[67] J.E. Hewitt, S.F. Thrush, Reconciling the influence of global climate phenomena on macrofaunal temporal dynamics at a variety of spatial scales, Glob. Chang. Biol. 15 (2009) 1911–1929.
[68] A. Törnroos, L. Pecuchet, J. Olsson, A. Gårdmark, M. Blomqvist, M. Lindegren, E. Bonsdorff, Four decades of functional community change reveals gradual trends and low interlinkage across trophic groups in a large marine ecosystem, Glob. Chang. Biol. 25 (2019) 1235–1246.
[69] S. Díaz, M. Cabido, Vive la difference: plant functional diversity matters to ecosystem, Trends Ecol. Evol. 16 (2001) 646–655.
[70] D.U. Hooper, F.S. Chapin, J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D.M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A.J. Symstad, J. Vandermeer, D.A. Wardle, Effects of biodiversity on ecosystem functioning; a consensus of current knowledge, Ecol. Monogr. 75 (2005) 3–35.
[71] S. Villéger, N.W.H. Mason, D. Mouillot, New multidimensional functional diversity indices for a multifaceted framework in functional ecology, Ecology 89 (2008) 2290–2301.
[72] D. Mouillot, N.A. Graham, S. Villeger, N.W. Mason, D.R. Bellwood, A functional approach reveals community responses to disturbances, Trends Ecol. Evol. 28 (2013) 167–177.
[73] S. Naeem, M. Loreau, P. Inchausti, Biodiversity and ecosystem functioning, the emergence of a synthetic ecological framework, in: S. Naeem, M. Loreau, P. Inchausti (Eds.), Biodiversity and Ecosystem Functioning, Oxford University Press, Oxford, 2002.
[74] O.L. Petchey, K.L. Evans, I.S. Fishburn, Low functional diversity and no redundancy in British avian assemblages, J. Anim. Ecol. 76 (2007) 977–985.
[75] O.L. Petchey, K.J. Gaston, Functional diversity: back to basics and looking forward, Ecol. Lett. 9 (2006) 741–758.
[76] E. Laliberté, P. Legendre, A distance-based framework for measuring functional diversity from multiple traits, Ecology 91 (2010) 299–305.
[77] N.W.H. Mason, D. Mouillot, W.G. Lee, J.B. Wilson, Functional richness, functional evenness and functional divergence: the primary components of functional diversity, Oikos 111 (2005) 112–118.
[78] M.A. Mouchet, S. Villéger, N.W.H. Mason, D. Mouillot, Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules, Funct. Ecol. 24 (2010) 867–876.
[79] E.J. Douglas, C.A. Pilditch, C. Kraan, L.A. Schipper, A.M. Lohrer, S.F. Thrush, Macrofaunal functional diversity provides resilience to nutrient enrichment in coastal sediments, Ecosystems 20 (2017) 1324–1336.
[80] R.V. Gladstone-Gallagher, H.R. Needham, A.M. Lohrer, C.J. Lundquist, C. A. Pilditch, Site-dependent effects of bioturbator-detritus interactions alter soft-sediment ecosystem function, Mar. Ecol. Prog. Ser. 569 (2017) 145–161.
[81] P. Hajializadeh, M. Safaie, R. Naderloo, M.G. Shojaei, J. Gammal, A. Villnäs, A. Norkko, Species composition and functional traits of macrofauna in different mangrove habitats in the Persian Gulf, Front. Mar. Sci. 7 (2020) 575480.
[82] O. Lam-Gordillo, R. Baring, S. Dittmann, Taxonomic and functional patterns of benthic communities in southern temperate tidal flats, Front. Mar. Sci. 8 (2021) 723749.
[83] M.G. Shojaei, L. Gutow, J. Dannheim, A. Schröder, T. Brey, Long-term changes in ecological functioning of temperate shelf sea benthic communities, Estuar. Coast. Shelf. Sci. 249 (2021).
[84] D.S. Clare, L.A. Robinson, C.L.J. Frid, Community variability and ecological functioning: 40 years of change in the North Sea benthos, Mar. Environ. Res. 107 (2015) 24–34.
[85] C.L.J. Frid, Temporal variability in the benthos: does the sea floor function differently over time? J. Exp. Mar. Biol. Ecol. 400 (2011) 99–107.
[86] C.L.J. Frid, B.A. Caswell, Is long-term ecological functioning stable: the case of the marine benthos? J. Sea Res. 98 (2015) 15–23.
[87] T.H. Pearson, R. Rosenberg, Macrobenthic succession in relation to organic enrichment and pollution of the marine environment, Oceanogr. Mar. Biol. Annu. Rev. 16 (1978) 229–311.
[88] A. Villnäs, A. Norkko, Benthic diversity gradients and shifting baselines: implications for assessing environmental status, Ecol. Appl. 21 (2011) 2172–2186.
[89] A. Lohrer, S. Thrush, M. Gibbs, Bioturbators enhance ecosystem function through complex biogeochemical interactions, Nature 431 (2004) 1092–1095.
[90] E.J. Douglas, A.M. Lohrer, C.A. Pilditch, Biodiversity breakpoints along stress gradients in estuaries and associated shifts in ecosystem interactions, Sci. Rep. 9 (2019) 17567.
[91] O. Lam-Gordillo, J. Huang, A. Barcelo, J. Kent, L.M. Mosley, D.T. Welsh, S. L. Simpson, S. Dittmann, Restoration of benthic macrofauna promotes biogeochemical remediation of hostile sediments; an in situ transplantation experiment in a eutrophic estuarine-hypersaline lagoon system, Sci. Total. Environ. 833 (2022) 155201.
[92] J.W. Oldman, K.P. Black, A. Swales, M.J. Stroud, Prediction of annual average sedimentation rates in an estuary using numerical models with verification against core data – Mahurangi Estuary, New Zealand, Estuar. Coast. Shelf. Sci. 84 (2009) 483–492.
[93] S.F. Thrush, J. Halliday, J.E. Hewitt, A.M. Lohrer, The effects of habitat loss, fragmentation, and community homogenization on resilience in estuaries, Ecol. Appl. 18 (2008) 12–21.
[94] M. Gibbs, G. Funnell, S. Pickmere, A. Norkko, J. Hewitt, Benthic nutrient fluxes along an estuarine gradient: influence of the pinnid bivalve Atrina zelandica in summer, Mar. Ecol. Prog. Ser. 288 (2005) 151–164.
[95] Hewitt, J.E., Hailes S.F., and B.L. Greenfield. 2014. Protocol for processing, identification and quality assurance of New Zealand marine benthic invertebrate samples. Prepared for Northland Regional Council:36.
[96] K.E. Ellingsen, N.G. Yoccoz, T. Tveraa, J.E. Hewitt, S.F. Thrush, Long-term environmental monitoring for assessment of change: measurement inconsistencies over time and potential solutions, Environ. Monit. Assess. 189 (2017) 1–16.
[97] Greenfield, B.L., S. Hailes, F. MacLean, R. Peart, G.B. Read, B. Marshall, and S. Mills. 2023. Protocol for the identification of benthic estuarine and marine macroinvertebrates: a guide for parataxonomists. C-SIG Coastal Taxonomic Resource Tool. 40 p + appendix.
[98] WoRMS. 2023. World register of marine species.
[99] Drylie, T.P. 2021. Marine ecology state and trends in Tāmaki Makaurau /Auckland to 2019. State of the environment reporting Auckland Council technical report. TR2021/09.
[100] D.P. Sartory, Spectrophotometric Analysis of Chlorophyll a in Freshwater Phytoplankton Report No. TR 115, Hydrological Research Institute, Department of Environment Affairs, Pretoria, 1982, p. 163.
[101] Gee, G.W., and J.W. Bauder. 1986. Particle-size analysis. Methods Soil Analysis: Part 1 Physical and Mineralogical Methods 5:383–411.
[102] R Core Team. R: A language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria, 2022.
[103] Laliberté, E., P. Legendre, and B. Shipley. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology R package version 1.0-12.

[104] S. de Juan, J. Bremner, J. Hewitt, A. Törnroos, M.C. Mangano, S. Thrush, H. Hinz, Biological traits approaches in benthic marine ecology: dead ends and new paths, Ecol. Evol. 12 (2022) e9001.
[105] O. Lam-Gordillo, A.M. Lohrer, J. Hewitt, S. Dittmann, NZTD - the New Zealand trait database for shallow-water marine benthic invertebrates, Sci. Data 10 (2023) 502.
[106] O. Lam-Gordillo, R. Baring, S. Dittmann, Establishing the South Australian Macrobenthic Traits (SAMT) database: A trait classification for functional assessments, Ecol. Evol. 10 (2020) 14372–14387.
[107] P. van der Linden, J. Patrício, A. Marchini, N. Cid, J.M. Neto, J.C. Marques, A biological trait approach to assess the functional composition of subtidal benthic communities in an estuarine ecosystem, Ecol. Indic. 20 (2012) 121–133.
[108] Taiyun, W., and S. Viliam. 2021. R package 'corrplot': visualization of a correlation matrix (Version 0.92).
[109] J. Fox, S. Weisberg, An R Companion to Applied Regression. Third Edition, Sage, Thousand Oaks CA, 2019.
[110] S.N. Wood, Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models, J. R. Stat. Soc. Ser. B Stat. Methodol. 73 (2011) 3–36.
[111] S.N. Wood, Generalized Additive Models: An Introduction with R, Chapman and Hall/CRC, 2017.
[112] H. Wickham, ggplot2: Elegant Graphics For Data Analysis, Springer-Verlag, New York, 2016. ISBN 978-3-319-24277-4.
[113] Simpson, G. 2024. gratia: graceful ggplot-based graphics and other functions for GAMs fitted using mgcv. R package version 0.9.0.
[114] Lüdecke, D. 2023. sjPlot: data visualization for statistics in Social science. R package version 2.8.14.
[115] F. Cook, R.O. Smith, M. Roughan, N.J. Cullen, N. Shears, M. Bowen, Marine heatwaves in shallow coastal ecosystems are coupled with the atmosphere: insights from half a century of daily in situ temperature records, Front. Clim. 4 (2022) 1012022.
[116] Oliver, E.C.J., J.A. Benthuysen, S. Darmaraki, M.G. Donat, A.J. Hobday, N.J. Holbrook, R.W. Schlegel, and SG. A. 2021. Marine heatwaves.
[117] E.C.J. Oliver, M.G. Donat, M.T. Burrows, P.J. Moore, D.A. Smale, L.V. Alexander, J.A. Benthuysen, M. Feng, A.S. Gupta, A.J. Hobday, N.J. Holbrook, S.E. Perkins-Kirkpatrick, H.A. Scannell, S.C. Straub, T. Wernberg, Longer and more frequent marine heatwaves over the past century, Nat. Commun. 9 (1) (2018) 1324.
[118] E.J. Douglas, O. Lam-Gordillo, S.F. Hailes, A.M. Lohrer, V.J. Cummings, Characterising intertidal sediment temperature gradients in estuarine systems, Estuar. Coast. Shelf. Sci. 309 (2024) 108968.
[119] M.J. Greig, N.M. Ridgway, B.S. Shakespeare, Sea surface temperature variations at coastal sites around New Zealand, N. Z. J. Mar. Freshwater Res. 22 (1988) 391–400.
[120] D.R. Schiel, S.A. Lilley, P.M. South, J.H. Coggins, Decadal changes in sea surface temperature, wave forces and intertidal structure in New Zealand, Mar. Ecol. Prog. Ser. 548 (2016) 77–95.
[121] M.J. Uddstrom, N.A. Oien, On the use of high-resolution satellite data to describe the spatial and temporal variability of sea surface temperatures in the New Zealand region, J. Geophys. Res. Oceans 104 (1999) 20729–20751.
[122] P. Jacobs, J. Pitarch, J.C. Kromkamp, C.J. Philippart, Assessing biomass and primary production of microphytobenthos in depositional coastal systems using spectral information, PLoS One 16 (2021) e0246012.
[123] R. Savelli, V. Le Fouest, M. Becker, G. Perrois, F. Rousset, C. Dupuy, M. Simard, D. Menemenlis, Warming could shift the phenological responses of benthic microalgae in temperate intertidal zones, Commun. Earth. Environ. 5 (2024) 606.
[124] J. Zhong, Y. Guo, Z. Liang, Q. Huang, H. Lu, J. Pan, P. Li, P. Jin, J. Xia, Adaptation of a marine diatom to ocean acidification and warming reveals constraints and trade-offs, Sci. Total Environ. 771 (2021) 145167.
[125] T.S. Bianchi, R. Dawson, P. Sawangwong, The effects of macrobenthic deposit-feeding on the degradation of chloropigments in sandy sediments, J. Exp. Mar. Biol. Ecol. 122 (1988) 243–255.
[126] Y. Huot, M. Babin, F. Bruyant, C. Grob, M.S. Twardowski, H. Claustre, Relationship between photosynthetic parameters and different proxies of phytoplankton biomass in the subtropical ocean, Biogeosciences 4 (2007) 853–868.
[127] D. Chilton, D.P. Hamilton, I. Nagelkerken, P. Cook, M.R. Hipsey, R. Reid, M. Sheaves, N.J. Waltham, J. Brookes, Environmental flow requirements of estuaries: providing resilience to current and future climate and direct anthropogenic changes, Front. Environ. Sci. 9 (2021) 764218.
[128] O. Lam-Gordillo, G.L. Petersen, S.F. Hailes, K. Carter, N.H. Salmond, L. McCartain, M. Ferries, B. Greenfield, E.J. Douglas, R. Hattingh, T. Drylie, B. Shanahan, A.M. Lohrer, Extreme weather event causes contrasting macrobenthic disturbance-recovery dynamics in two New Zealand estuaries, Next Res. 2 (2025) 100726.
[129] O. Lam-Gordillo, A.M. Lohrer, E. Douglas, S. Hailes, K. Carter, B. Greenfield, Scale-dependent influence of multiple environmental drivers on estuarine macrobenthic crustaceans, Front. Mar. Sci. 10 (2023) 1292849.
[130] J.I. Ellis, D. Clark, J. Atalah, W. Jiang, C. Taiapa, M. Patterson, J. Sinner, J. Hewitt, Multiple stressor effects on marine infauna: responses of estuarine taxa and functional traits to sedimentation, nutrient and metal loading, Sci. Rep. 7 (2017) 12013.
[131] J.E. Hewitt, J.I. Ellis, S.F. Thrush, Multiple stressors, nonlinear effects and the implications of climate change impacts on marine coastal ecosystems, Glob. Chang. Biol. 22 (2016) 2665–2675.
[132] J.C.F. Pardo, A.E. Poste, H. Frigstad, C.O. Quintana, H.C. Trannum, The interplay between terrestrial organic matter and benthic macrofauna: framework, synthesis, and perspectives, Ecosphere 14 (2023).
[133] G.R. Lopez, J.S. Levinton, Ecology of deposit-feeding animals in marine sediments, Q. Rev. Biol. 62 (1987) 235–260.
[134] M. Szczepanek, M.J. Silberberger, K. Koziorowska-Makuch, E. Nobili, M. Kędra, The response of coastal macrobenthic food-web structure to seasonal and regional variability in organic matter properties, Ecol. Indic. 132 (2021) 108326.
[135] A. Norkko, V.J. Cummings, S. Thrush, J. Hewitt, T. Hume, Local dispersal of juvenile bivalves: implications for sandflat ecology, Mar. Ecol. Prog. Ser. 212 (2001) 131–144.
[136] A. Norkko, S.F. Thrush, J.E. Hewitt, V.J. Cummings, J. Norkko, J.I. Ellis, G. A. Funnell, D. Schultz, I. MacDonald, Smothering of estuarine sandflats by terrigenous clay: the role of wind-wave disturbance and bioturbation in site-dependent macrofaunal recovery, Mar. Ecol. Prog. Ser. 234 (2002) 23–42.
[137] D.E. Clark, F. Stephenson, J.E. Hewitt, J.I. Ellis, A. Zaiko, A. Berthelsen, R. H. Bulmer, C.A. Pilditch, Influence of land-derived stressors and environmental variability on compositional turnover and diversity of estuarine benthic communities, Mar. Ecol. Prog. Ser. 666 (2021) 1–18.
[138] A.G. Dvoretsky, V.G. Dvoretsky, Effects of environmental factors on the abundance, biomass, and individual weight of juvenile red king crabs in the Barents Sea, Front. Mar. Sci. 7 (2020) 726.
[139] U. Schückel, M. Beck, I. Kröncke, Spatial variability in structural and functional aspects of macrofauna communities and their environmental parameters in the Jade Bay (Wadden Sea Lower Saxony, southern North Sea), Helgol. Mar. Res. 67 (2012) 121–136.
[140] J. Gammal, J. Hewitt, J. Norkko, A. Norkko, S. Thrush, Does the use of biological traits predict a smooth landscape of ecosystem functioning? Ecol. Evol. 10 (2020) 10395–10407.
[141] C. Henseler, M.C. Nordström, A. Törnroos, M. Snickars, L. Pecuchet, M. Lindegren, E. Bonsdorff, Coastal habitats and their importance for the diversity of benthic communities: a species- and trait-based approach, Estuar. Coast. Shelf. Sci. 226 (2019) 106272.
[142] V.N. Kokarev, A.A. Vedenin, A.B. Basin, A.I. Azovsky, Taxonomic and functional patterns of macrobenthic communities on a high-arctic shelf: a case study from the Laptev Sea, J. Sea Res. 129 (2017) 61–69.
[143] F.J. Murillo, B. Weigel, M. Bouchard Marmen, E. Kenchington, Y. Dong, Marine epibenthic functional diversity on Flemish Cap (north-west Atlantic)—Identifying trait responses to the environment and mapping ecosystem functions, Divers. Distrib. 26 (2020) 460–478.