



Extreme weather event causes contrasting macrobenthic disturbance-recovery dynamics in two New Zealand estuaries

Orlando Lam-Gordillo^{a,*}, Grady L. Petersen^a, Sarah F. Hailes^a, Kelly Carter^a,
Nichola H. Salmond^b, Lisa McCartain^a, Michal Ferries^a, Barry Greenfield^a,
Emily J. Douglas^a, Reuben Hattingh^a, Tarn Drylie^c, Becky Shanahan^d,
Andrew M. Lohrer^a

^a National Institute of Water and Atmospheric Research, Hamilton, New Zealand

^b Coastal and Marine, Science, Policy and Information Unit, Waikato Regional Council, Hamilton, New Zealand

^c Research & Evaluation Unit, Auckland Council, Auckland, New Zealand

^d Freshwater & Marine Science Team, Hawkes Bay Regional Council, Napier, New Zealand

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ABSTRACT

Extreme weather events, such as cyclones, are predicted to increase in frequency and intensity due to the rapidly changing climate. Cyclones can drastically alter estuarine ecosystems, affecting ecosystem function and service delivery. This study aimed to evaluate the effects of an extreme weather event, Cyclone Gabrielle, on estuarine macrobenthic communities and estuarine ecosystem functions in two estuaries in New Zealand. The data was analysed from prior to the passage of the cyclone (Before), soon after its passage (Event), and in the year after its passage (After), focusing on intertidal soft-sediment macroinvertebrate communities and metrics (e.g., abundance, richness, diversity, functional traits, functional richness, functional redundancy) and the overall relationship between macrobenthic fauna, their functional traits, and environmental conditions (i.e., estuarine ecosystem functioning). Results showed that the extreme weather event caused significant changes in macrobenthic metrics over time. Decreases in key macrobenthic metrics were coincident with the Event and After the cyclone in one of the estuaries. Results also showed changes in estuarine ecosystem functioning as macrobenthic metrics and functional traits changed, with reduced and weaker relationships found After the cyclone, suggesting potential disruption of key processes, functions, and services that estuarine ecosystems provide. Yet, these findings provide evidence of relatively rapid and nearly complete recovery to pre-cyclone ecological conditions within a year of the extreme weather event. More frequent extreme weather events might surpass the recovery periods of macrobenthic organisms and the environment, leading to greater impacts.

1. Introduction

Marine ecosystems around the world are threatened by the rapidly changing climate, driving profound environmental changes at multiple scales and directly impacting marine species and ecosystems [1–4]. Future predictions suggest that global warming will continue to accelerate sea-level rise and sea-ice melting, while increasing the frequency and severity of extreme weather events such as marine heatwaves, storms, and tropical cyclones [2,5,6]. This is likely to affect the distribution and structure of marine assemblages that underpin essential processes, functions, and services in marine ecosystems [7–11].

Estuarine ecosystems are some of the most productive, exploited, and threatened ecosystems in the world [12–14]. These ecosystems, which are at the interface between freshwater and marine environmental domains, are considered hotspots for biodiversity and biogeochemical cycling. They provide a range of ecosystem functions (e.g., nutrient cycling, carbon storage) and ecological services (e.g., coastal protection, food production), and contribute to our culture [15–17]. Yet, estuarine ecosystems are affected by multiple past and ongoing human-induced pressures such as increasing inputs of sediments, inorganic nutrients, and other pollutants, which are challenging the health and functioning of estuaries, the services these ecosystems provide, and the biota they

* Corresponding author.

E-mail address: orlando.lam-gordillo@niwa.co.nz (O. Lam-Gordillo).

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host [13,14,18,19].

Estuarine ecosystems are also affected by aperiodic extreme weather events (cyclones, storms, heatwaves), periodic natural cycles (seasons, tides, climate oscillations), and broader climatic drivers (e.g., changes in air and water temperatures and sea levels), which together affect estuarine functioning [20–23]. Yet, some of the fluctuations and frequencies of “natural” disturbance events and cycles (e.g., storms, heatwaves) have been altered by human activities [14,24,25]. For example, anthropogenic CO₂ emissions are thought to be contributing to greater frequencies and intensities of storms [2,5,26] and there is evidence of increased landslides, flooding, sediment loading, and nutrient inputs to estuaries following storms because of poor catchment management (e.g., hillslope deforestation, straightening of river channel networks, increased paving of roads/urban centres) [27–29]. Given our understanding of the deleterious effects of fine terrigenous sediment deposition and elevated turbidity in estuaries [30–33], there is concern about the health of estuaries in a future with more intense and frequent storm events.

Extreme weather events—particularly hurricanes, typhoons, and cyclones that make landfall—can have numerous and widespread impacts on land and at the coast [26,34,35]. While the immediate focus during storms is rightly protecting city infrastructure and human lives, extreme weather events can also affect estuarine ecosystems and the values and services they provide to society over the longer term. The focus of this research was understanding the effects of extreme weather events on estuarine benthic communities and the potential consequences of changes in biodiversity on ecosystem functions. Despite a few recent investigations of extreme weather impacts on estuarine ecosystems [26,34,35], the effects of extreme weather events on macrobenthic fauna and their functional traits are not well described in New Zealand (no prior studies to our knowledge). Macrobenthic fauna and their functional traits are vital indicators of ecological change in estuaries, as they respond sensitively to disturbances [36–38]. They can reveal shifts in habitat conditions, nutrient dynamics, and ecosystem functioning [37,38], making them essential for assessing the resilience and health of estuarine environments under increasing climate variability. However, this lack of understanding limits our ability to predict responses to future events and determine the long-term resilience and recovery potential of estuarine ecosystems in a changing world.

In February 2023, the Tropical Cyclone Gabrielle struck New Zealand (Figure S1). The cyclone affected the northern parts of the North Island of New Zealand as a Category 2 tropical cyclone with high winds, waves, and mild storm surge [39]. Central and eastern areas of the North Island were most predominantly affected by heavy rainfall. Rainfall totals of 350–501 mm over a 24-hr period (peak ~30 mm/h) were recorded, causing major flooding, landslides, coastal erosion, and widespread destruction of property and natural landscapes [39]. As a result of the landslides and erosion, extremely high rates of sediment loading occurred during and in the immediate aftermath of the storm (estimated up to 300 million tonnes of eroded sediment in the Hawkes Bay region [40], with tens to hundreds of cm of terrigenous sediment deposited in flood plains near the coast, on the intertidal flats in some estuaries, and offshore with deposits of sediment up to 1 m thickness in subtidal areas [27,39,41]).

Here, the effects of Cyclone Gabrielle on estuarine macrobenthic communities and estuarine ecosystem functioning were investigated. This study leveraged existing estuarine macrobenthic data collected before and after the cyclone to improve the understanding of how macrobenthic communities and estuarine functioning respond to extreme weather events. The aim of this study was to (i) evaluate changes in macrobenthic communities, their functional trait composition, and functional diversity before and after the extreme weather event, and to (ii) investigate the effects of Cyclone Gabrielle on the relationship between macrobenthic fauna, functional traits, and environmental conditions (i.e., ecosystem functioning). It was hypothesised that macrobenthic fauna and functional traits will be less abundant and

diverse, and ecosystem functioning will be reduced after the cyclone due to extreme environmental stress, but that it would recover within ~1 year [34].

2. Materials and methods

2.1. Study area

The study was carried out across two estuaries in the North Island of New Zealand: Ōkura Estuary in the Auckland region and Ahuriri Estuary in the Hawkes Bay region (Fig. 1). Ōkura Estuary is a small shallow estuary (600 m wide; 1.35 km² total area) located on the east coast of New Zealand (Fig. 1). Sediment grain size on the flats in Ōkura Estuary ranges from sandy (>90 % fine and very fine sands near the mouth) to relatively muddy (>25 % silt-clay) closer to the site of freshwater influx. Recent assessments of Ōkura Estuary suggest effects of gradual increases in sediment mud content over time [42–44]. Another assessment suggested that organic matter content in sediment has remained steady (1–2 %) and that chlorophyll *a* has increased slightly over time (2010–2020) [22].

Ahuriri Estuary is a shallow, microtidal estuary located in Hawke's Bay, New Zealand [45]. Ahuriri Estuary is a remnant of the Ahuriri Lagoon or Napier Inner Harbour. This estuary has two crossing roads, the lower estuary has broad tidal flats and shallow channels. The middle estuary is a narrow stop banked stretch with islands and channels. The upper estuary swings northward above the confluence with the Taipo Stream around the base of Poraiti Hills. Several small streams enter the estuary through ponding and wetlands areas [46]. Low to moderate levels of sediment mud content (<25 %) are reported in the lower section of the estuary, while higher levels of mud (>60 %) have consistently occurred in the middle and upper sections of the estuary over time (2013–2018). Sediment chlorophyll *a* content is high (9000 mg/m³) in the lower section of the estuary and lower in the upper section of the estuary [47].

2.2. Data collection

Macrobenthic data collection, processing of samples, sorting, and identifications followed standard protocols for New Zealand [48], with strict quality assurance, quality control procedures, and taxonomic harmonization [48–51]. Macrobenthic data were collected from 10 sites throughout Ōkura Estuary (Fig. 1). Eight of the 10 sites were sampled in February 2023 (two days after Cyclone Gabrielle), and all 10 sites were sampled eight months later in October 2023. Sampling on the other dates was limited to three sites per date (and not necessarily the same three sites each date) based on Auckland Council's State-of-the-Environment monitoring program requirements (Table 1). In Ahuriri estuary, macrobenthic data were collected from four sites (Fig. 1). Two of the four sites were sampled from 2020 to 2024, including March 2023 (<1 month after Cyclone Gabrielle). Sampling dates at the other two sites varied based on the requirements of Hawkes Bay Regional Council's monitoring program (Table 1). At each of the sampling sites, six (Ōkura Estuary) or 12 (Ahuriri estuary) replicate sediment samples for assessing macrobenthic fauna were collected by hand using a 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, Table S1) using specialised taxonomic keys and following standardised protocols [49], and counted.

To assist the investigations into responses of macrobenthic fauna to extreme weather events, a variety of ancillary environmental information from the tidal flats for use as explanatory variables were collected. Samples for analysis of sediment Chlorophyll *a* content (Chl *a*; mg/g), organic matter content (OM; %), and grain size distribution (% dry weight in different fractions) were collected together with the macrobenthic samples. Sediment samples for Chl *a*, OM, and grain size

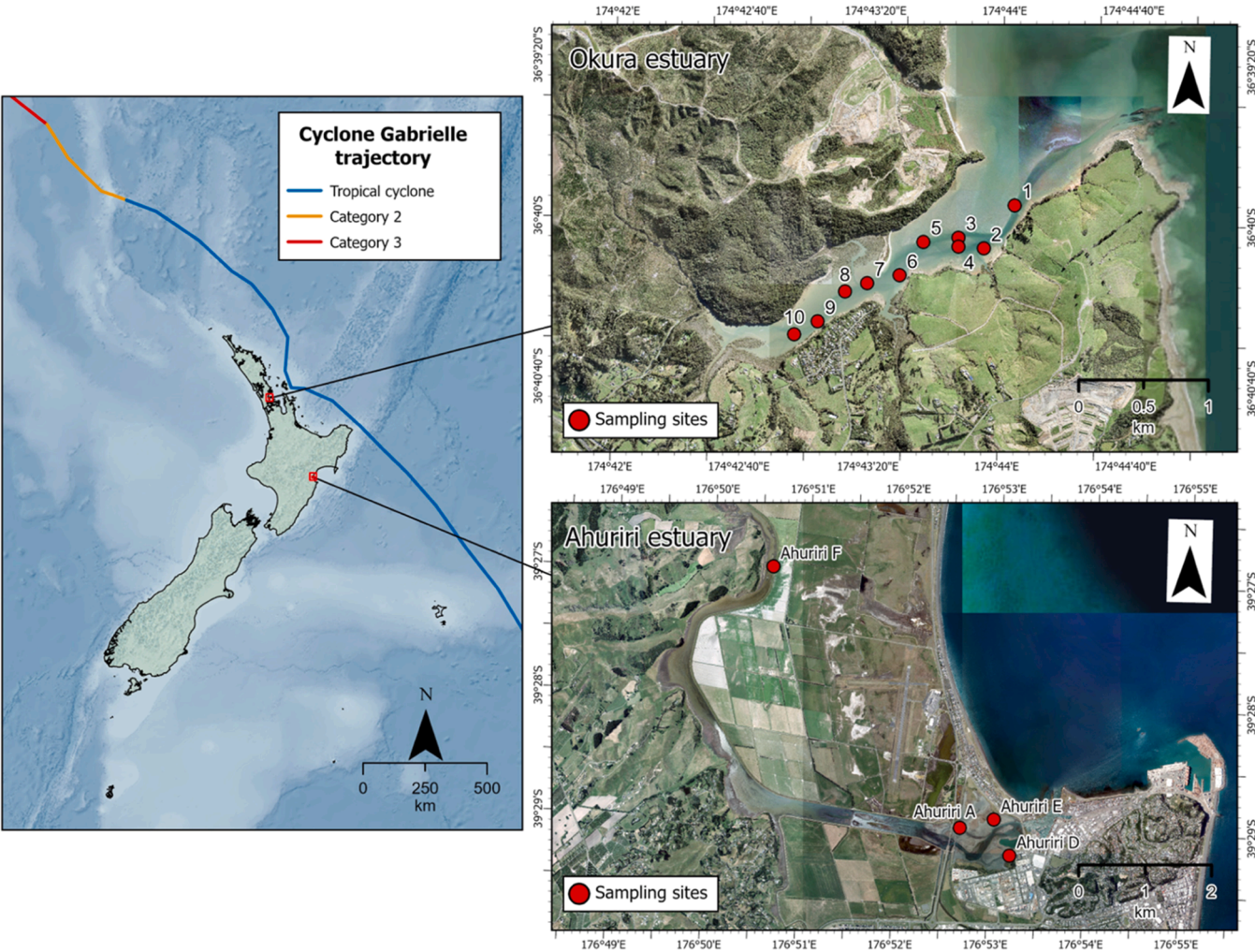


Fig. 1. Map of the study area showing the macrobenthic sampling sites along the two study cases Ōkura and Ahuriri estuaries in the North Island of New Zealand. The trajectory and intensity of the Cyclone Garbielle is also showed.

Table 1

Summary table showing the sampling (x) event at each site in Ōkura and Ahuriri estuaries for this study. The categorical time-period classification based on the extreme weather event is showed in different colours. Blue: Before (Ōkura: Apr-22, Oct-22; Ahuriri: Feb-20, Feb-21, Feb-22, Jan-23), Orange: Event (Ōkura: Feb-23, Ahuriri: Mar-23), Green: After (Ōkura: Apr-23, Oct-23; Ahuriri: May-23, Aug-23, Nov-23, Feb-24).

Estuary	Site	Feb-20	Feb-21	Feb-22	Apr-22	Oct-22	Jan-23	Feb-23	Mar-23	Apr-23	May-23	Aug-23	Oct-23	Nov-23	Feb-24
Ōkura	1				x			x					x		
	2							x					x		
	3					x		x		x			x		
	4			x				x					x		
	5							x					x		
	6												x		
	7					x		x		x			x		
	8							x					x		
	9			x		x				x			x		
	10							x					x		
Ahuriri	A	x	x	x			x		x		x	x		x	x
	D	x	x	x			x				x	x		x	x
	E	x	x	x							x	x		x	x
	F	x	x				x		x		x				

distribution were collected using a smaller PVC corer (26 mm diameter, 20 mm deep core) at the same sites and times as macrofaunal data collection, with the exception of OM samples, which were not collected from sites in Ahuriri estuary in March 2023. Each replicate for Chl *a*, OM, and grain size was an amalgam of six cores collected at positions spanning the site [44]. 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* [52]. 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 distribution, samples

were homogenised and then digested in ~ 9 % hydrogen peroxide until frothing ceased. Samples were wet sieved through 2000 µm, 500 µm, 250 µm, 125 µm, and 63 µm mesh sieves. Pipette analysis was used to find the proportion of the <63 µm fraction that is >3.9 µm (silt) and <3.9 µm (clay) using Stoke's Law. All fractions were then dried at 60 °C until a constant weight was achieved (fractions are weighed at ~ 40 h and then again at 48 h) to obtain the percentage weight of gravel/shell hash (>2000 µm), coarse sand (500–2000 µm), medium sand (250–500 µm), fine sand (125–250 µm), very fine sand (63–125 µm), silt (3.9 – 63 µm), and clay (<3.9 µm). Mud content is calculated as the sum of the silt and clay content.

Daily rainfall (mm) and maximum (Tmax, °C) and minimum (Tmin= n, °C) temperature records were also collected as drivers that potentially influence estuarine macrobenthic communities. Rainfall data and maximum (Tmax) and minimum (Tmin) temperature were extracted from ClifLo (New Zealand's National Climate Database - <https://cliflo.niwa.co.nz/>) at the stations "North Shore Albany" and "Napier Aero Aws" as they were the closest stations to Ōkura and Ahuriri estuaries, respectively.

2.3. Data analysis

Analysis of time as a continuous variable (i.e., as a time-series) was not possible because of differing sampling frequencies and non-matching sampling dates at the sites in the two estuaries (Table 1). Therefore, for all the analyses, a categorical time-period classification based on the extreme weather event was implemented: "Before", "Event", and "After" (Table 1). Data from multiple sites and times in each estuary were grouped into the "Before" and "After" categories, whereas "Event" was characterised by samples collected on a single date in each estuary (Ōkura: eight sites sampled on Feb-2023; Ahuriri: 2 sites sampled on Mar-2023; Table 1). Thus there were unequal numbers of data points in the different time and site categories, and samples were collected on different dates in the two estuaries, which likely limited the power of the analyses to detect statistically significant differences.

Environmental conditions (i.e., Chl a, OM, Mud, Rainfall, Tmax) were visually analysed (e.g., boxplots, density-plots, line-plots,) to understand the environmental trends over time in Ōkura and Ahuriri estuaries. To investigate changes in environmental conditions over time (Before, Event, After), univariate PERMutational Analysis Of Variance (PERMANOVA) was used based on Euclidean distance for the single variables, permutation of residuals under a reduced model, sums of squares type III, and 9999 permutations [53]. Multiple pair-wise tests were conducted if the fixed factor (time category) was significant to identify which groupings contributed to differences from PERMANOVA main tests.

To evaluate the effects of the extreme weather event on macrobenthic fauna, traditional and functional metrics were calculated using the packages 'vegan' [54] and 'FD' [55] in R software [56]. Traditional diversity metrics included the analysis of taxonomic richness (S) and Shannon-Wiener diversity (H', log e), as well as the total abundance (N) of macrofauna for each site sampled in Ōkura and Ahuriri estuaries. Functional metrics were calculated based on the selection of a suite of five functional traits and 22 traits modalities (Table 2). The functional traits selected describe behavioural, morphological, and physiological attributes of the organisms, which can be influenced by sedimentary conditions. Trait information was retrieved from The New Zealand Trait Database for shallow-water marine benthic invertebrates – NZTD [57]. The NZTD uses a fuzzy coding procedure, assigning scores from 0 to 1 to each taxon, with 0 being no affinity and 1 being high affinity to a trait for details see [57]. Functional metrics including Functional Richness (FRic) and Functional Redundancy (FR) were calculated. FRic tracks the amount of functional space occupied by a community [37,58], and FR is calculated as the ratio between Functional Diversity (FD – measured as the RaoQ entropy) and H', when the ratio between FD and H' decreases, FR increases and vice versa [37,59]. In addition, Community-level

Table 2
List of the functional traits and traits-modalities selected based on their response to extreme weather events modified from [57]. Acronyms are used in Fig. 6.

Functional trait	Trait modalities	Acronyms
Bioturbator	Biodiffusor	Bdiff
	Bioirrigator	Birrig
	No bioturbation	Nbio
	Surface modifier	Sumo
Body size	Large (20 mm)	Lar
	Medium (5–20 mm)	Med
	Small (0.5–5 mm)	Sma
Feeding mode	Deposit feeder	Defe
	Filter suspension	Fisus
	Grazer/scraper	Graz/Sc
	Predator	Pred
	Scavenger/opportunist	Scav
	Sub-surface deposit feeder	Ssdefe
Living habit	Burrower	Att
	Crawler	Burr
	None	Free
	Swimmer	Parc
Sediment position		Tubdw
	Attached	
	Benthopelagic	Atta
	Epibenthic	Be-pel
	Deeper >3cm	Epi
	Surface shallow <3cm	Deep

Weighted Means of trait values (CWM) were calculated to compare trait expression across Ōkura and Ahuriri estuaries. To facilitate trend visualisation, univariate and functional metrics were presented as boxplots constructed using the package 'ggpubr' [60]. To investigate the effects of the extreme weather event in metrics (abundance, S, H', FRic, FR, and CWM) across Ōkura and Ahuriri estuaries, PERMANOVA was used to analyse variation among factors, based on Euclidean distances for the single macrobenthic metrics, permutation of residuals under a reduced model, sums of squares type III, and 9999 permutations [53]. In addition, multiple pair-wise tests were conducted if the fixed factor (time) was significant to identify which groupings contributed to differences from PERMANOVA main tests.

To assess community structure differences between times, bootstrapped non-Metric Multidimensional Scaling (nMDS) sample ordination plots were created for each estuary. Macrobenthic community data were fourth root transformed, and a Bray-Curtis similarity resemblance was applied [53]. To test for differences in community structure, PERMANOVA tests were performed using fourth root transformed macrofauna data, Bray Curtis Similarities, permutation of residuals under a reduced model, sums of squares type III and 9999 permutations (Anderson et al., 2008). PERMANOVAs, Pairwise tests, and bootstrapped nMDS plots were performed in PRIMER v7 with PERMANOVA+ add on software [53].

The effects of Cyclone Gabrielle on ecosystem functioning, i.e., the relationship between macrobenthic fauna, functional traits, and environmental conditions (fourth corner analysis) was investigated using Generalized Linear Latent Variable Models (GLLVMs) with the R package "gllvm" [61]. GLLVM extends the basic GLM, handles overdispersion data, includes latent variables to capture the correlation between species, and considers fourth-corner terms to account for species-traits-environment interactions [61,62]. GLLVMs were constructed for fitting multivariate data using a negative binomial distribution as the best fit model (lowest Akaike information criterion—AIC) [61]. Level plots were performed for visualizing the interactions between taxa-traits and environmental variables obtained with the GLLVMs using the R package "lattice" [63].

3. Results

3.1. Environmental conditions

Environmental conditions differed in the two estuaries and across the three-time categories (Fig. 2). For example, in Ōkura Estuary, concentrations of Chl *a* were highest before the storm (i.e., Before) and were significantly lower in its aftermath (i.e., Event), increasing again in the months after the storm (i.e., After) but not to the level they were beforehand (PERMANOVA $p < 0.05$, Fig. 2a). In contrast, Chl *a* concentrations in Ahuriri were significantly higher during Event than they were After (PERMANOVA $p < 0.05$, Fig. 2d). Organic content in sediment did not differ across the three time periods in Ōkura Estuary, although the lowest percentages of OM were recorded during Event (PERMANOVA $p > 0.05$, Fig. 2b). In Ahuriri Estuary, organic content was significantly lower in the After period, relative to Before (PERMANOVA $p < 0.05$, Fig. 2e). The mud content of the sediment in Ōkura Estuary was significantly lower Before, relative to the Event and After periods

(PERMANOVA $p < 0.05$, Fig. 2c). In Ahuriri Estuary, mud content was highest during Event, intermediate during Before, and lowest After (PERMANOVA $p < 0.05$, Fig. 2f).

Climatic conditions were similar in both estuaries (Fig. 3). Rainfall totals exhibit marked seasonality in the regions of both estuaries, with the highest and lowest rainfall totals in July-Aug (winter) and Jan-Feb (summer), respectively (Fig. 3). In the two years prior to the extreme weather event, annual average rainfall was 95 mm and 75 mm in Ōkura and Ahuriri estuaries, respectively. Rainfall totals were markedly higher, during the Event in Ōkura and Ahuriri estuaries, exceeding 700 mm and 300 mm over an 15 day period, respectively (Fig. 3). The range between temperature maximum (Tmax) and minimum (Tmin) over time was higher in Ōkura Estuary compared to Ahuriri Estuary (Fig. 3). The variability of Tmax and Tmin was relatively similar in both estuaries overtime, and effects of the Event were not obvious in the temperature records (Fig. 3).

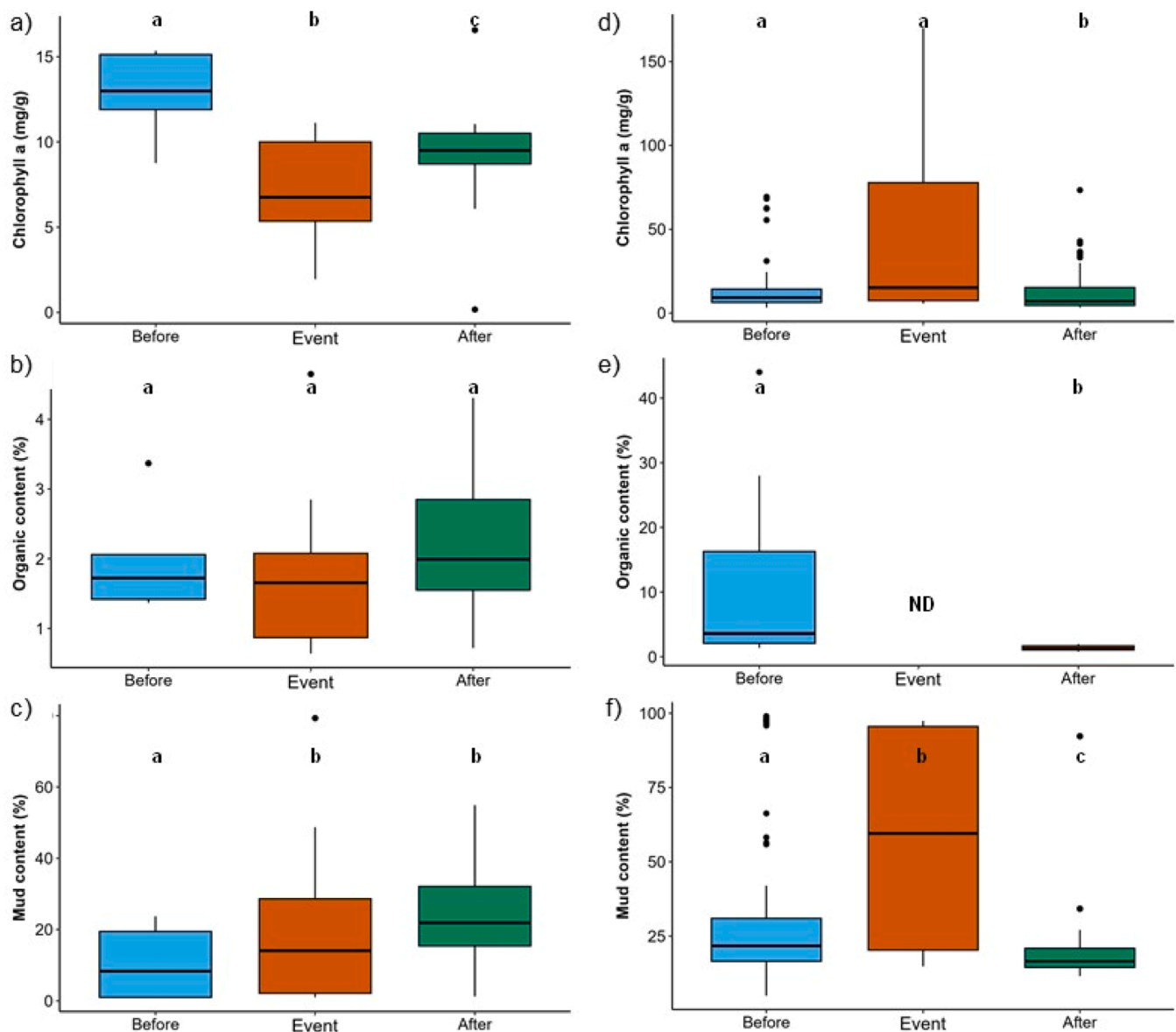


Fig. 2. Box plots showing the environmental conditions chlorophyll *a*, organic matter content, mud content, and rainfall and maximum temperature over time in Ōkura (a-c) and Ahuriri (d-f) estuaries. Significant differences between times are showed with letters a, b, c. Colour in boxplot showed the categorical time-period classification based on the extreme weather event. ND: No data.

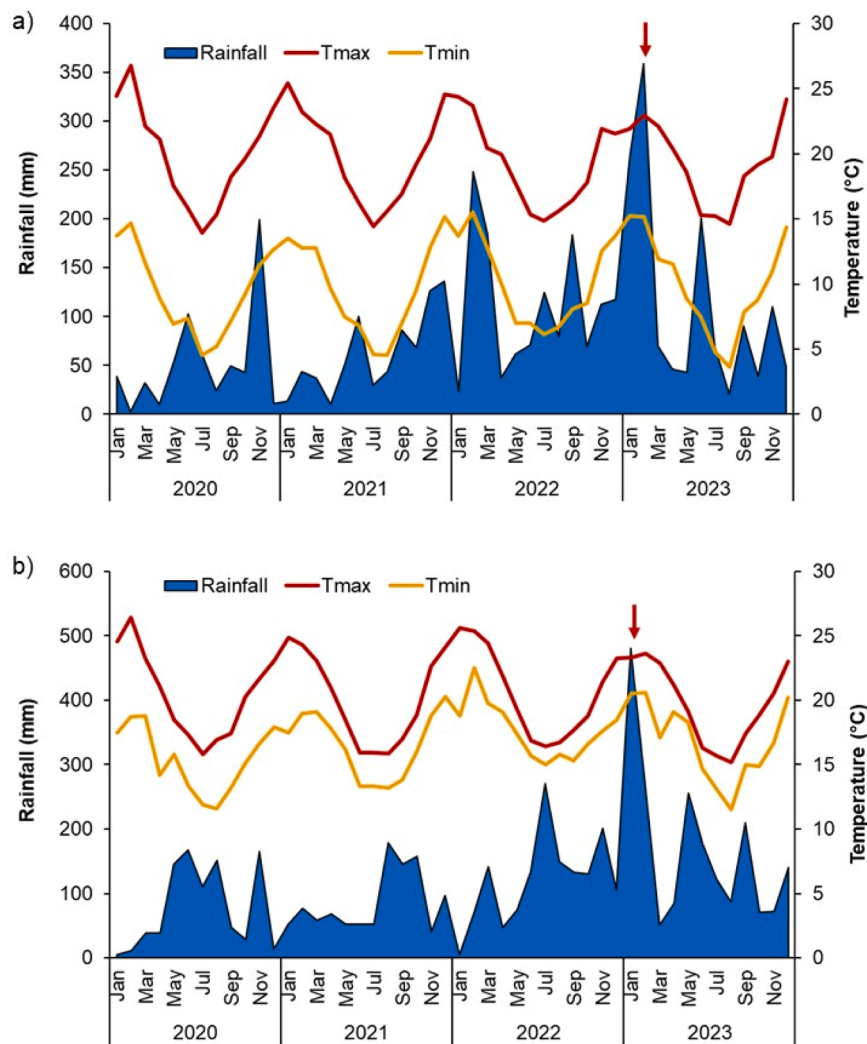


Fig. 3. Plots showing the climatic conditions rainfall and maximum and minimum temperature over time in Ōkura (a) and Ahuriri (b) estuaries. Extreme weather event, Cyclone Gabrielle, struck New Zealand from 12–15 of February 2023 (denoted with a red arrow).

3.2. Effects of the extreme weather event on macrobenthic metrics

Macrobenthic abundance in Ōkura and Ahuriri estuaries differed significantly by time category ($p < 0.05$; Table 3; Fig. 4a, 4d). In Ōkura Estuary, mean abundance was significantly lower during the Event period, relative to the Before and After periods, while macrobenthic abundance in Ahuriri estuary was significantly higher After, relative to the Before and Event periods (PERMANOVA $p < 0.05$; Fig. 4a, 4d).

Macrobenthic richness also differed significantly by time period in both estuaries ($p < 0.05$; Table 3; Fig. 4b, 4e). In Ōkura Estuary the lowest richness was during Event and higher Before and After (with no difference between the Before and After periods), while in Ahuriri Estuary, the lowest richness was found Before the storm, richness was intermediate during Event, and richness was highest After the storm (PERMANOVA $p < 0.05$; Fig. 4b, 4e).

Significant differences in macrobenthic diversity were also identified across time in both estuaries ($p < 0.05$; Table 3; Fig. 4c, 4f). In Ōkura Estuary, the highest mean diversity was recorded Before, which was significantly higher than during Event (but not significantly higher than during the period After the storm) (PERMANOVA $p < 0.05$; Fig. 4c). In Ahuriri Estuary, macrobenthic diversity was significantly higher during the Event and After periods than it was in the period Before the storm (PERMANOVA $p < 0.05$; Fig. 4f).

For macrobenthic community structure, significant differences

among the categories of Before, Event, and After were detected in both estuaries (Fig. 5). The bootstrapped nMDS plot for Ōkura and Ahuriri estuaries revealed three well-defined clusters that were related to the time categories, with all significantly different from each other (PERMANOVA $p < 0.05$; Fig. 5). Connecting the clusters according to their chronological order (i.e., Before-Event-After) revealed similar temporal trajectories in the two estuaries (Fig. 5).

Significant differences in Functional Richness were found across time in both estuaries ($p < 0.05$; Table 3; Fig. 6a, 6c). In Ōkura Estuary, FRic was significantly lower during Event than it was Before and After (PERMANOVA $p < 0.05$; Fig. 6a), while in Ahuriri Estuary, FRic was marginally higher during Event than it was Before (not statistically different at $p = 0.05$) and highest during the period After the storm (PERMANOVA $p < 0.05$; Fig. 6c). In contrast, Functional Redundancy did not differ across time periods in either estuary ($p > 0.05$; Table 3; Fig. 6b, 6d).

On average, the most expressed functional trait modalities in both estuaries, based on Community-level Weighted Means (CWM) analyses of trait values, were 'surface modifier' (bioturbation; proportional contribution: Ōkura - 0.56 %, Ahuriri - 0.49 %), 'small body size' (<5 mm; proportional contribution: Ōkura - 0.55 %), 'large body size' (>20 mm; proportional contribution: Ahuriri - 0.52 %), 'deposit feeder' (feeding mode; proportional contribution: Ōkura - 0.47 %, Ahuriri - 0.39 %), 'burrower' (living habit; proportional contribution: Ōkura -

Table 3

Test results from univariate one-way fixed factor PERMANOVA to compare abundance, number of taxa (richness), Shannon diversity index (H'), Functional Richness (FRic), and Functional Redundancy (FR) across times in Ōkura and Ahuriri estuaries. Significant differences are shown in bold.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Abundance						
<i>Ōkura</i>						
Time	2.00	29,359.00	14,679.00	6.16	0.0021	9868
Residuals	159.00	378,880.00	2382.90			
Total	161.00	408,240.00				
<i>Ahuriri</i>						
Time	2	875,200.00	437,600.00	44.11	0.0001	9940
Residuals	333	3303,200.00	9919.60			
Total	335	4178,400.00				
Richness						
<i>Ōkura</i>						
Time	2	652.01	326.01	17.94	0.0001	5240
Residuals	159	2889.30	18.17			
Total	161	3541.30				
<i>Ahuriri</i>						
Time	2	2373.00	1186.50	112.54	0.0001	4538
Residuals	333	3510.70	10.54			
Total	335	5883.70				
H'						
<i>Ōkura</i>						
Time	2	4.63	2.32	12.10	0.0001	9947
Residuals	159	30.45	0.19			
Total	161	35.08				
<i>Ahuriri</i>						
Time	2	16.13	8.07	33.16	0.0001	9955
Residuals	333	81.00	0.24			
Total	335	97.13				
Functional Richness						
<i>Ōkura</i>						
Time	2	1214.60	607.32	3.38	0.0362	9954
Residuals	159	28,605.00	179.90			
Total	161	29,819.00				
<i>Ahuriri</i>						
Time	2	5853.70	2926.90	25.94	0.0001	9953
Residuals	333	37,574.00	112.83			
Total	335	43,427.00				
Functional Redundancy						
<i>Ōkura</i>						
Time	2	30.651	15.33	2.88	0.0631	9948
Residuals	159	844.81	5.31			
Total	161	875.46				
<i>Ahuriri</i>						
Time	2	114.54	57.27	2.46	0.0873	9965
Residuals	333	7746.50	23.26			
Total	335	7861.00				

0.60 %, Ahuriri – 0.56 %), and ‘surface sediment’ position (shallow <3 cm; proportional contribution: Ōkura - 0.66 %, Ahuriri – 0.55 %) (Fig. 6).

Eleven of the 23 trait modalities analysed showed significant differences between time periods in Ōkura Estuary, and 17 of the 23 traits modalities differed significantly by time in Ahuriri Estuary (Table 4; Fig. 7). Differences in functional trait expression were idiosyncratic comparing both estuaries (Fig. 7, Table S2-S3). For example, in Ōkura Estuary, the CWM of the trait modalities ‘bioturbator’, ‘surface modifier’, ‘medium body size’, and ‘free living / surface crawler’ showed significant differences when comparing Before and After, and between Event and After, with indications of increases After the storm (Fig. 7a-c; Table S2). In contrast, trait modalities such as ‘no bioturbation’, ‘small body size’, ‘deposit feeder’, ‘burrower’, and ‘surface shallow’ showed significant decreases comparing Before, Event, and After (Fig. 7a-c; Table S2). In Ahuriri Estuary, the trait modalities ‘bioturbator’, ‘bio-irrigator’, ‘medium body size’, ‘filter / suspension feeders’, ‘burrower’, and ‘surface shallow’ showed significant differences Before and After the cyclone with decreasing trends of trait expression (Fig. 7d-f; Table S3). In contrast, the trait modalities ‘surface modifier’, ‘large and small body size’, ‘deposit feeder’, ‘sub-surface deposit feeder’, ‘free living / surface crawler’, ‘benthic-pelagic’, ‘epibenthic’, and ‘deeper than 3cm’ also showed significant differences between Before and After the cyclone but

with increasing trend in functional trait expression (Fig. 7d-f; Table S3). Across both estuaries, only the functional trait modality ‘Scavenger / Opportunistic’ significantly increased in trait expression from Before to After (Fig. 7d-f; Table S3).

3.3. Effects of the extreme weather event on ecosystem functioning

Significant relationships between the macrobenthic fauna, their functional traits, and the environmental conditions in the different time periods were identified in both estuaries (Fig. 8; Figure S2-S3). The strongest and weakest interactions between benthic macrofauna, traits, and environmental conditions were identified Before and After the storm, respectively (Fig. 8). Four of the five functional traits and several of their modalities showed significant interactions with environmental conditions in the three time periods in both Ōkura and Ahuriri estuaries (Fig. 8).

Before the storm in Ōkura Estuary, the trait modalities of ‘Deposit feeder’ and ‘Filter /suspension feeder’, but also all other feeding mode trait modalities, were strongly negatively correlated to Chl *a* and Mud, while positively correlated to OM (Fig. 8a). In contrast, the trait modalities ‘surface modifier’, ‘bioirrigator’, and ‘bioturbator’ were positively correlated to Chl *a* and Mud, with a negative correlation to OM (Fig. 8a). Correlations between all the trait modalities of Sediment

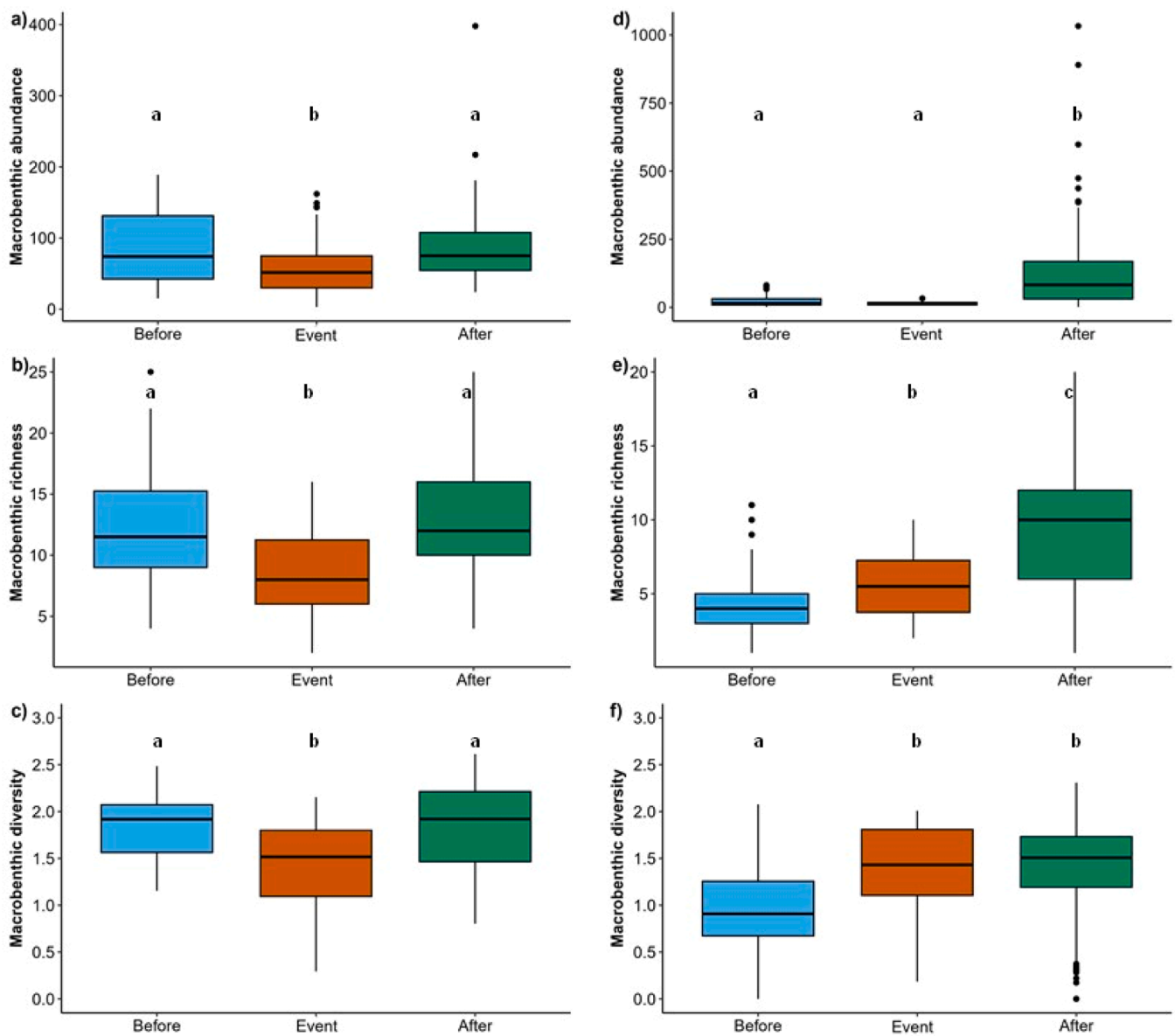


Fig. 4. Box plots showing the macrobenthic abundance, richness and Shannon diversity index over time in Ōkura (a-c) and Ahuriri (d-f) estuaries. Significant differences between times are showed with letters a, b, c. Colour in boxplot showed the categorical time-period classification based on the extreme weather event.

position and Chl *a*, OM, and Mud were also observed but less pronounced, while weak correlations between all modalities of Bioturbation and Rainfall and T_{max} were also identified (Fig. 8a). Fewer and weaker relationships between macrobenthic fauna, their functional traits, and the environmental conditions were identified during Event compared to Before the storm (Fig. 8a). The strongest correlations were found between the trait modalities 'attached', 'epibenthic', 'deeper than 3cm', and 'surface shallow <3cm' and OM (negative) and Mud (positive) (Fig. 8a). All the Feeding mode and Bioturbation trait modalities were also correlated to Chl *a*, OM, and Mud (positively with Chl *a* and OM, and negatively with Mud) (Fig. 8a). The relationships between macrobenthic fauna, their functional traits, and the environmental conditions observed After the cyclone were weaker compared to Before and Event (Fig. 8a). Correlations between all Feeding mode and Bioturbation trait modalities with Chl *a*, OM, and Mud were identified, with Chl *a* and Mud showing negative correlations and OM positive correlations (Fig. 8a).

Before the storm in Ahuriri Estuary, strong negative correlations were identified between Chl *a* and all the trait modalities of Bioturbation

and Living habit, between OM and all the trait modalities of Feeding mode and Sediment position, and between Mud, Rainfall, and T_{max} and all the modalities of Bioturbation (Fig. 8b). In contrast, strong positive relationships were found between Rainfall and T_{max} and all trait modalities from Feeding mode, Living habit, and Sediment position. Mud and OM also showed positive relationships with all Living habit trait modalities (Fig. 8b). Similar to Ōkura Estuary, fewer and weaker relationships between macrobenthic fauna, their functional traits, and the environmental conditions were identified during Event compared to Before the cyclone (Fig. 8b). The strongest negative correlations were found between Rainfall and 'biodiffuser', 'bioirrigator', and 'surface modifier' trait modalities. Additionally, Rainfall negatively correlated to all of the Feeding mode trait modalities and the living position modalities of 'epibenthic', 'deeper than 3 cm', and 'surface 0–3 cm' (Fig. 8b). Chl *a* and Mud showed positive correlations to 'biodiffuser', 'bioirrigator', and 'surface modifier', all of the Feeding mode trait modalities, and the living position modalities of 'epibenthic', 'deeper than 3 cm', and 'surface 0–3 cm' (Fig. 8b). The relationships between macrobenthic fauna, their functional traits, and the environmental conditions

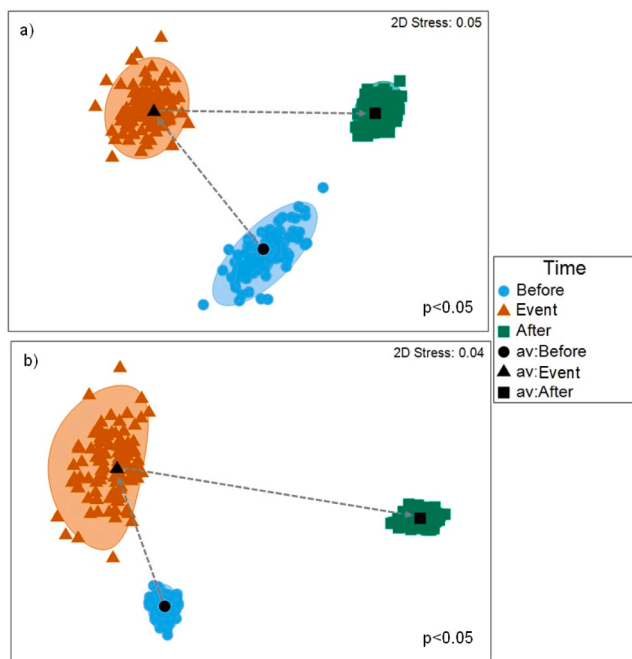


Fig. 5. Bootstrapped non-Metric Multidimensional Scaling (nMDS) plots for benthic communities over time in a) Ōkura and b) Ahuriri estuaries. Colours correspond to sampling events Before (blue), Event (orange), and After (green) the extreme weather event. Arrows shows the trajectory of change over time. Black symbols indicate the average for each group.

observed After the storm were fewer and weaker relative to Before and Event (Fig. 8b). Mud content in sediment showed the strongest negative correlation with the 'attached' trait modality and positive correlations with 'burrower', 'free living / surface crawling', and 'tube dwelling' trait modalities (Fig. 8b).

4. Discussion

The effects of extreme weather events such as cyclones on estuarine ecosystems are complex, multifaceted, and vary in magnitude and duration depending on the nature of the event, the physical characteristics of the estuary, and the resilience of their biota. There is evidence that anthropogenic influences on our climate are enhancing natural processes and increasing the frequency and intensity of storms and cyclones [2,5,25], causing significant modifications in the functions and services estuarine ecosystems provide. This study investigated the effects of an extreme weather event, Cyclone Gabrielle, on estuarine macrobenthic communities and estuarine ecosystem functioning of two estuaries in New Zealand. The results of this study revealed significant changes in sedimentary characteristics (i.e., chlorophyll *a*, organic matter, mud content), macrobenthic communities, abundance, richness, diversity, and FRic in three periods: prior to the storm (i.e., Before), in the <30 days after the storm (i.e., Event), and in the 1–12 months after the storm (i.e., After). Overall, macrobenthic metrics decreased during the Event and After the cyclone in Ōkura Estuary, while in Ahuriri Estuary the macrobenthic metrics remained similar Before, during the Event, and After the cyclone. We also depicted changes in the relationships between macrobenthic abundance, functional traits, and environmental conditions over time as a proxy of changes in ecosystem functioning in the intertidal habitats of the two estuaries, Ōkura and

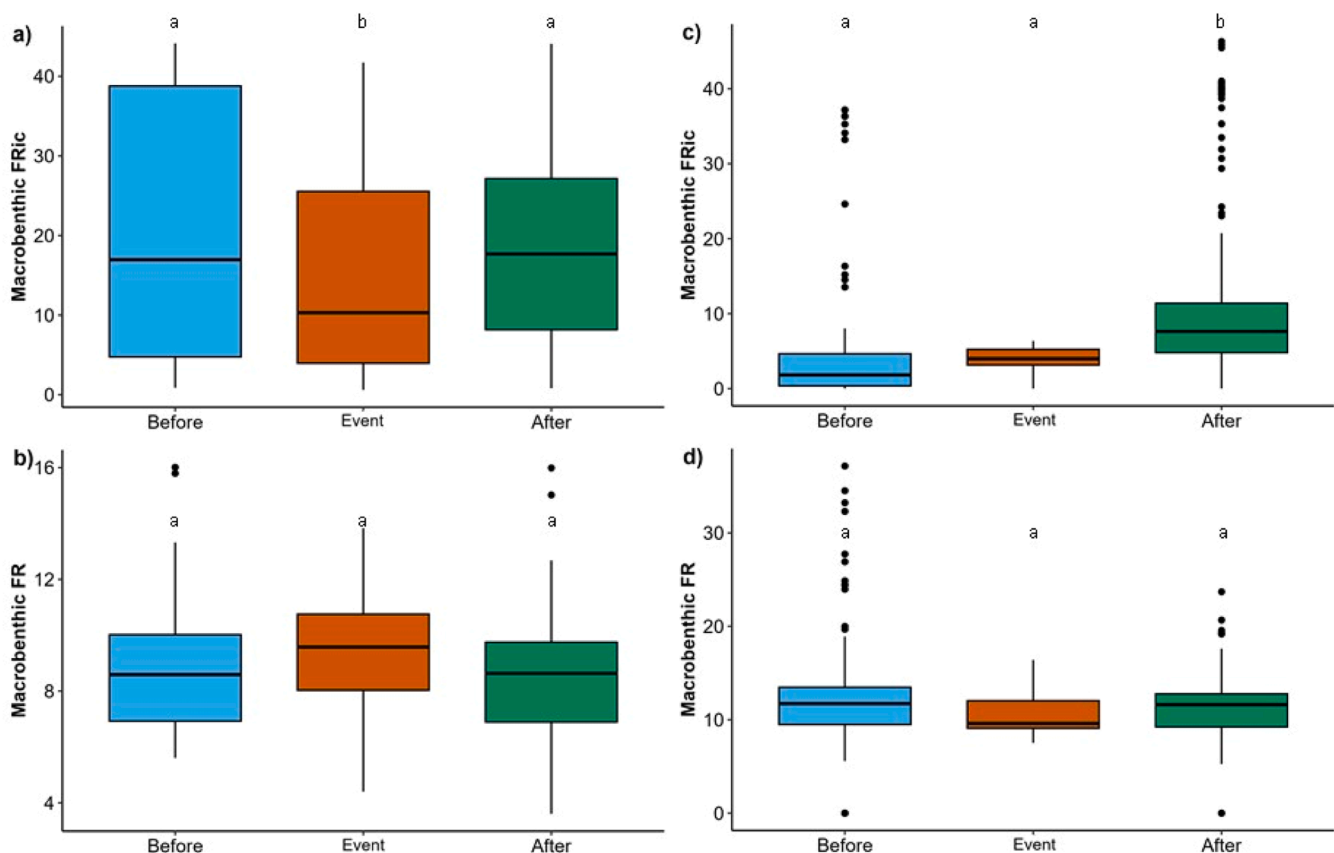


Fig. 6. Box plots showing the Functional Richness (FRic) and Functional Redundancy (FR – ratio between FD and H', when the ratio decreases, FR increases) over time in Ōkura (a-b) and Ahuriri (c-d) estuaries. Significant differences between times are shown with letters a, b, c. Colour in boxplot showed the categorical time-period classification based on the extreme weather event.

Table 4
Test results from univariate one-way fixed factor PERMANOVA to compare functional trait modalities across times in Ōkura and Ahuriri estuaries. Significant differences are shown in bold. NC: No computed.

Trait	Trait modality	Ōkura			Ahuriri		
		Pseudo-F	P(perm)	Unique perms	Pseudo-F	P(perm)	Unique perms
Bioturbator	Biodiffusor	5.6104	0.0044	9955	6.3295	0.0022	9946
	Bioirrigator	0.8504	0.4260	9948	61.4700	0.0001	9955
	No bioturbation	5.9873	0.0019	9958	1.5136	0.3228	90
	Surface modifier	5.2404	0.0068	9954	61.231	0.0001	9954
Body size	Large (>20 mm)	0.0625	0.9561	113	79.7660	0.0001	9936
	Medium (5–20 mm)	11.5390	0.0001	9956	5.4767	0.0053	9953
	Small (0.5–5 mm)	3.8465	0.0219	9965	147.0500	0.0001	9953
Feeding mode	Deposit feeder	8.6801	0.0003	9954	11.9900	0.0001	9959
	Filter/suspension	0.1824	0.8324	9950	52.3630	0.0001	9942
	Grazer/scraper	2.6525	0.0652	9961	23.3210	0.0001	9944
	Predator	5.8244	0.0040	9958	2.2827	0.0981	9960
	Scavenger/opportunist	7.3072	0.0016	9956	27.0180	0.0001	9955
	Sub-surface deposit feeder	0.5354	1.0000	115	8.6278	0.0072	9933
Living habit	Attached	2.1328	0.1170	9951	NC	NC	NC
	Burrower	12.6570	0.0001	9951	57.5100	0.0001	9954
	Free living/surface crawler	13.409	0.0001	9957	57.6930	0.0001	9961
	Parasite/commensal	2.6987	0.0592	9950	2.7139	0.0756	9921
	Tube dwelling	1.4929	0.2287	9946	0.0606	0.9433	9954
Sediment position	Attached	0.9629	0.3737	9955	1.9649	0.1451	9936
	Benthic-pelagic	2.6493	0.0708	270	82.8690	0.0001	9953
	Epibenthic	2.5504	0.0781	9944	18.3060	0.0002	9950
	Deeper >3cm	2.4978	0.0874	9942	29.5970	0.0001	9941
	Surface shallow <3cm	7.4045	0.0009	9930	18.9470	0.0001	9952

Ahuriri.

Previous studies have reported significant alterations to environmental conditions such as sediment texture, sediment grain size, organic matter content in sediment, salinity, and sediment transport in coastal ecosystems as consequence of cyclones or major storms [26,35,64,65], often leading to immediate disruption and long-term ecological changes in these ecosystems. It was identified that the environmental conditions in Ōkura and Ahuriri estuaries were different Before and After Cyclone Gabrielle struck. Increased mud content in the sediment and rainfall was found during the Event period. Rainfall decreased in the following months, yet concentrations of mud content and organic matter in sediment remained high over the longer term in Ōkura Estuary, which aligned with previous studies suggesting persisting long-term environmental modifications, especially in soft-sediment dominated systems [26,34,35].

Evidence of contrasting patterns in macrobenthic metrics (i.e., abundance, richness, diversity, CWM, FRic) over time in the study estuaries was found. In Ōkura Estuary, macrobenthic fauna abundance, richness, diversity, functional trait expression (CWM), and FRic, showed typical disturbance-recovery patterning, aligning with our hypothesis of decreased values in the immediate aftermath of the Event (relative to Before) and increased values again over the longer term as the macrofauna recover. However, in Ahuriri Estuary, macrobenthic metrics were higher in the aftermath of the storm and continued increasing over the longer term, contrary to our hypothesis.

Decreased macrobenthic abundance, richness, diversity, CWM, and FRic following extreme weather events has been previously reported in other parts of the world, suggesting that storms, cyclones, and hurricanes modify sediment characteristics, including grain size and availability of organic matter, which are vital factors for the stability of macrobenthic communities [26,34,35,64]. It has been also suggested that decreases in macrobenthic metrics could be caused by accretion and redistribution of sediments, burying fauna in highly depositional zones in estuaries and advecting them away from highly erosional zones [26, 31,66]. Macrobenthic decreases could be also explained by the numerous and widespread impacts of cyclones in coastal ecosystems. For example, hypoxia from increased sediment inputs and hyposaline conditions caused by high volumes of freshwater discharge into estuaries following intense rainfall events can drive declines in

macrobenthic fauna [26,31,34] and could potentially explain the patterns found in Ōkura Estuary. However, it is unlikely that hyposaline conditions persisted for more than a few days after the storm in Ōkura Estuary due to its high amount of intertidal area and high flushing rate (i.e., almost the entire volume of the estuary is flushed out to sea on every outgoing tide).

In Ōkura Estuary, the decrease in macrobenthic abundance, richness, diversity, and FRic in the immediate aftermath of the storm (i.e., Event) was followed by evidence of recovery to pre-cyclone values in the After period. The recovery pattern may be explained by the arrival of new recruits. The storm occurred during the warm summer season when many of the species are reproducing, which would have bolstered recolonisation rates [34,67,68]. Most estuarine macrobenthic fauna are adapted to high-energy and dynamic conditions, which may enable them to recover relatively rapidly from storm events. Yet, potential changes in the abundance, distribution, and composition of macrobenthic communities could persist for years without full recovery [26, 34,65,69], with important implications for the ecological functioning of estuaries.

The increases in macrobenthic abundance, richness, diversity, and FRic in Ahuriri Estuary in the shorter and longer term after the storm were surprising. It is possible that Ahuriri, in which the lower estuary generally has gravelly and coarser sediment, was food limited prior to the storm, meaning that the high influx of sediment and organic matter to the estuary during the storm stimulated the macrofauna to a degree. It has also been reported that the volume of freshwater discharge to Ahuriri Estuary was so high during the storm that rates of sediment deposition within the estuary were low (i.e., most of the sediment transited through the estuary and was deposited offshore), which would have limited the amount of smothering and deposition-related physical disturbance at sites within the estuary [47,70,71]. Thus, greater organic food supplies and limited deleterious fine-sediment deposition may have contributed to increases in macrobenthic abundance, richness, diversity, and FRic [14,26,35,72], though this needs further investigation. Furthermore, changes in macrobenthic metrics are generally driven by multiple environmental, ecological, and evolutionary factors, such as duration and intensity of the extreme weather event, competition and reproduction [26,34].

It was also identified that Functional Redundancy (FR) was similar in

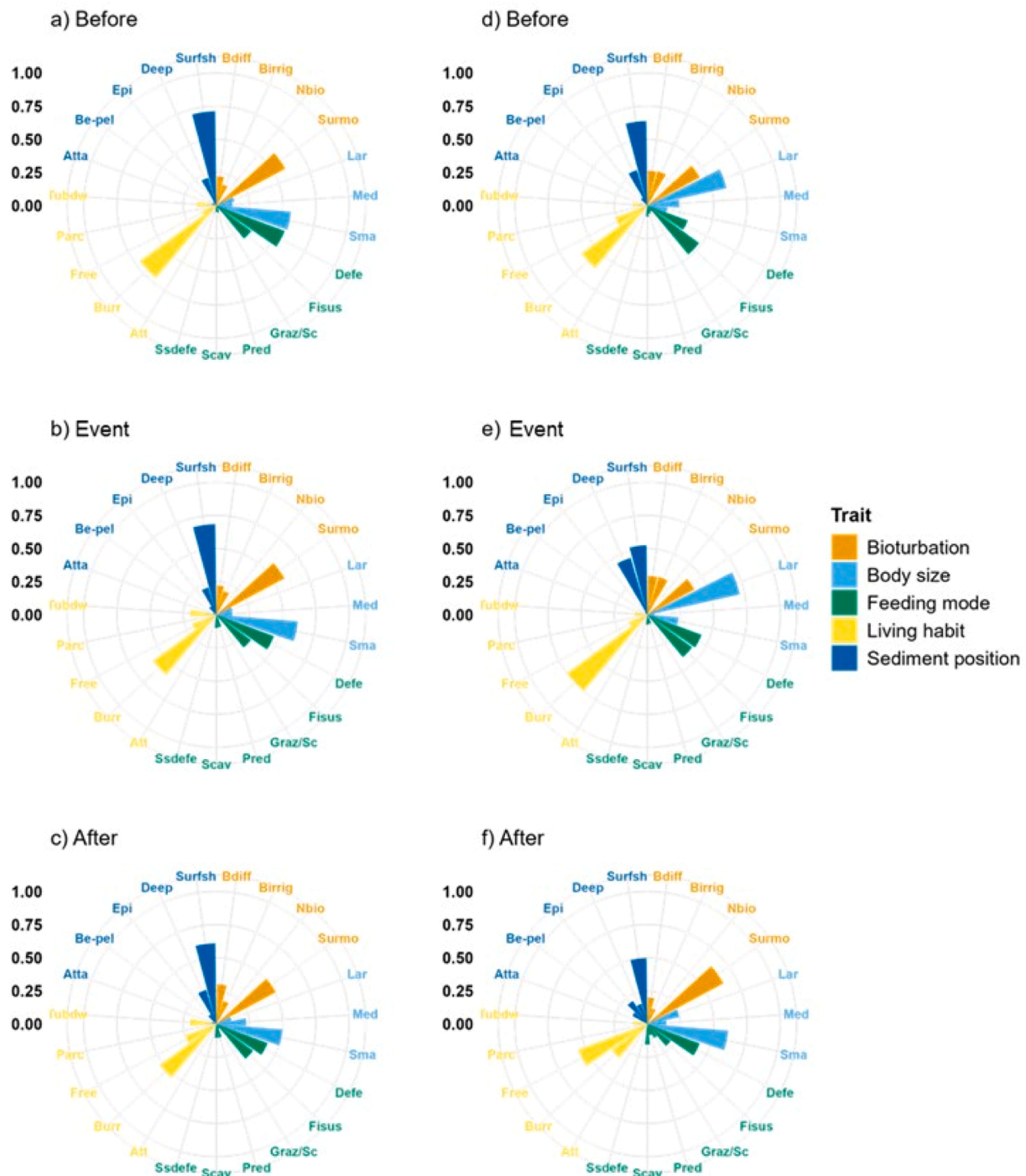


Fig. 7. Community-weighted means (CWM) of functional trait-modalities expression. Scale represents the percentage contribution to CWM recorded in Ōkura (a-c) and Ahuriri (d-f) estuaries over time. Trait modalities labels (acronyms) are defined in Table 2.

all three time periods assessed (i.e., Before, Event, After), indicating that despite potentially extreme environmental stress, the multiple taxa occupying the available functional trait space were able to maintain functionality [37,59,73,74]. This could also align with a previous investigation reporting that Ahuriri Estuary has low functional resilience, which could suggest that the functionality in this estuary was not worsened by the extreme weather event, but it was already poor and resulted in similarities between Before, Event, and After [75].

Climatic variability and natural periodic changes (e.g., seasons, tide cycles) could also influence the changes in macrobenthic metrics in both estuaries. However, our results showed that the climatic variability (i.e.,

seasonal and long-term average rainfall, Tmax, and Tmin) were relatively similar in both estuaries in the two years prior the extreme weather event. A previous study using long-term environmental and macrobenthic data showed that macrobenthic metrics can respond to unique combinations of multiple environmental drivers, with highly mixed (i.e., positive and negative) and site-dependent responses [22]. This is consistent with our findings of significant effects on macrobenthic metrics from an extreme weather that was anomalous to typical climatic and periodic variability.

Results from this study also suggest that, depending on macrobenthic composition, trait expression, and environmental conditions, some

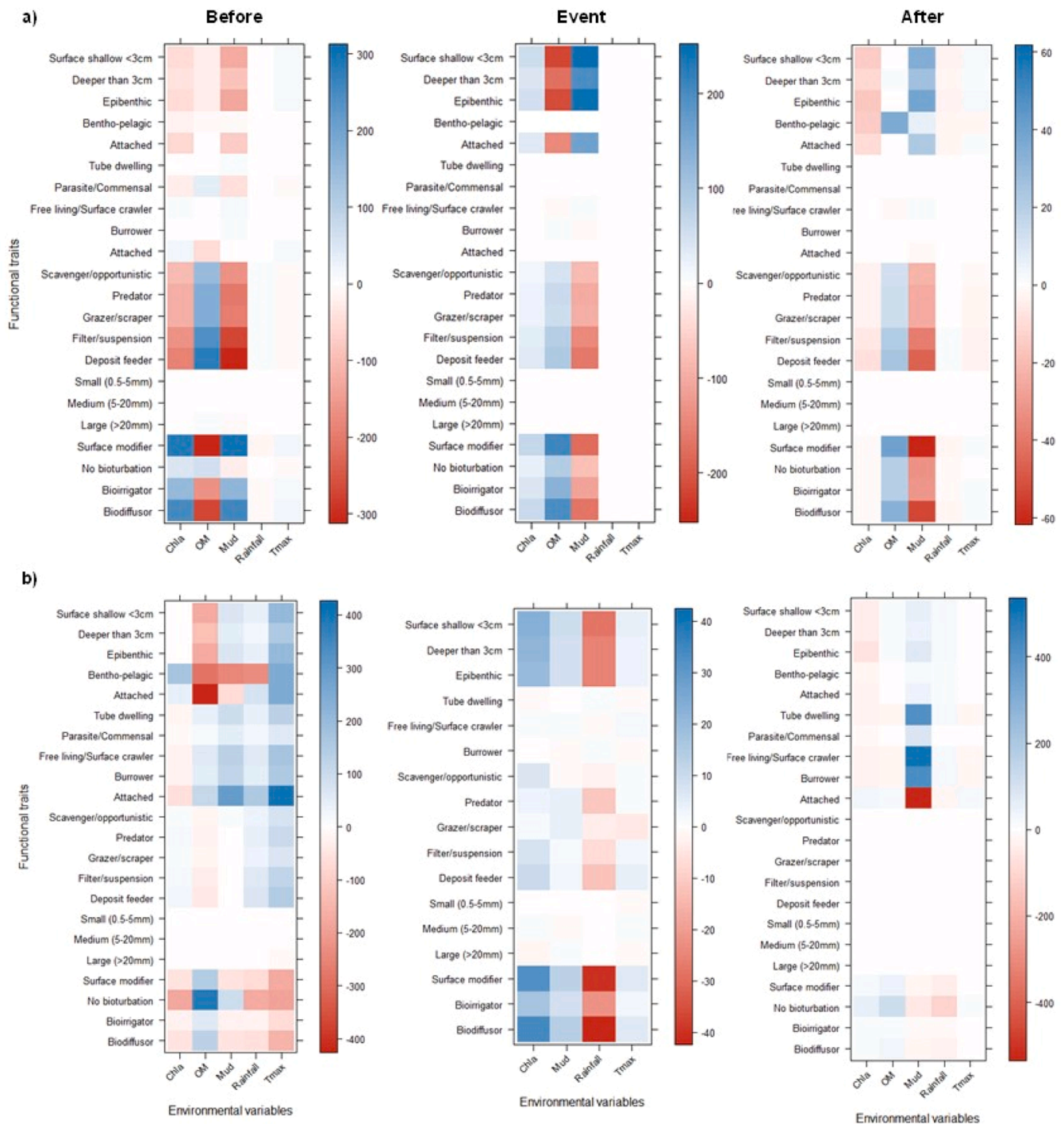


Fig. 8. Level plot for the fourth corner interaction (macrobenthic abundance, functional traits, and environmental variables) using NB-GLLVM showing the interactions in a) Ōkura and b) Ahuriri estuaries over time. The colour scale indicates significant interactions and magnitudes of the point estimates.

macrofauna mediated ecosystem functions may have changed in relation to the extreme weather event. In the absence of direct measurements (i.e., nutrient cycling, sediment transport, organic matter remineralization, productivity), insights into ecosystem functioning were inferred from knowledge of the linkages between taxa, traits and environmental conditions [17,37,76]. It was predicted that estuarine functioning (i.e., the relationship between macrobenthic abundance, their functional traits, and environmental conditions) would be reduced in the immediate aftermath of the storm, which aligned to the results of this study. It was identified that the strongest correlations between macrobenthic fauna, functional traits, and environmental conditions

Before the cyclone, relative to Event and After in both estuaries. Chl *a* was positively correlated with all trait modalities of Bioturbation, Feeding mode, and Living habit during the Event period in both estuaries, suggesting increased primary productivity and food availability, and potentially differentiation in the use of resources by the macrofauna [37,77,78].

Mud content in sediment was shown to be negatively correlated with all trait modalities in the Bioturbation and Feeding trait modes in Ōkura Estuary, suggesting that the high levels of Mud affected the feeding behaviours and sediment reworking potentials of macrofauna in this estuary. Fewer deposit feeders and burrowers could lead to reduced

nutrient cycling and less oxygenated sediments [38,79]. Yet, during the Event period in Ahuriri Estuary, the effects of Mud were observed to be weakly positive. Only the Living habit trait modality of 'Attached' was affected by Mud in Ahuriri Estuary.

Mud content in sediment is well recognised as a limiting condition for macrobenthic organisms [20,31,33,80–82]. Our results from Ōkura Estuary suggested that increased Mud in the longer term post storm decreased 'bioirrigator', 'deposit feeder', 'burrower', and 'surface shallow' macrobenthic organisms, likely leading to reduced sediment nutrient cycling, sediment oxygenation, and productivity [37,77,78]. Over the longer-term post storm in Ahuriri Estuary, we detected positive relationships between Chl *a* and Bioturbation, and between Mud content and 'burrower', 'free living', 'tube dwelling', and all Sediment position trait modalities. These results aligned with previous studies reporting that deposit feeders are generally dominant in muddy sediments with high levels of Chl *a* [37,83], as macrofaunal organisms feed on micro-phytobenthos [76,84]. Interestingly, macrobenthic body size was not correlated with any environmental variables, even though we identified significant increases in medium- and large sized organisms, and decreases in small sized organisms, in Ōkura and Ahuriri estuaries, respectively, in the After storm period. The implication is that larger organisms, which are known to have greater effects on processes such as nutrient cycling, sediment reworking and energy fluxes [16,77], may be more resilient to extreme weather events.

Evidence suggesting that the extreme weather event, cyclone Gabrielle, caused significant changes to macrobenthic metrics in Ōkura and Ahuriri estuaries was provided. Yet, predicting changes in macrobenthic communities and consequent effects on the functioning of estuarine ecosystems under future scenarios of increasing extreme weather events is still a challenge [5,6,26,34,35,85]. It is suggested that estuarine management efforts should consider the effects of increasing frequency and intensity of extreme weather events such as cyclones, as increasing on runoff from heavy rainfall could lead to higher nutrient loads, causing eutrophication and hypoxia, which can severely impact estuarine biota. Furthermore, other overlapping anthropogenic stressors could be acting at the same time. For example, sea level rise may threaten estuarine ecosystems by altering the salinity gradients and inundating habitats [86,87]. This can lead to the loss of critical habitats such as salt marshes and mangroves, which serve as nurseries for many marine species [87]. Therefore, to manage estuarine ecosystems effectively under these challenging conditions, adaptive management strategies are essential. These strategies should be flexible and responsive to changing conditions, for example (i) implementation of monitoring and early warning systems, (ii) restoring degraded habitats and conserving existing ones, (iii) managing upstream activities to reducing the impacts of pollution and sedimentation on estuarine ecosystems, and (iv) building infrastructure that can withstand extreme weather events.

5. Conclusion

Estuaries are increasingly affected by more frequent and intense weather events such as cyclones. This study investigated the effects of Cyclone Gabrielle on macrobenthic fauna and estuarine functioning in Ōkura and Ahuriri estuaries to provide a better understanding of both the immediate and longer-term responses of macrobenthic communities to extreme weather events. It was demonstrated that the extreme weather event caused significant changes to macrobenthic communities and environmental conditions in the intertidal habitats of the two estuaries. Decreases in macrobenthic metrics were driven by increases in rainfall (freshwater input) and sediment loads (Mud content in sediment). Estuarine ecosystem functions, indicated by changes in functional traits, also appeared to decrease after the cyclone, suggesting potential disruptions to key processes, functions, and services such as nutrient cycling, sediment reworking, and food web support. This study also showed that macrobenthic communities were able to recover fully or nearly fully within a year of the extreme weather event. However, it is

important to note that increasing frequency and severity of extreme weather events could overwhelm the ability of estuarine macrobenthos to recover, presenting new challenges for estuarine conservation and management.

CRedit authorship contribution statement

Orlando Lam-Gordillo: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Grady L. Petersen:** Writing – review & editing, Validation, Project administration, Methodology, Funding acquisition, Data curation. **Sarah F. Hailes:** Writing – review & editing, Methodology, Investigation, Data curation. **Kelly Carter:** Writing – review & editing, Methodology, Investigation, Data curation. **Nichola H. Salmond:** Writing – review & editing, Resources, Methodology, Investigation, Data curation. **Lisa McCartain:** Writing – review & editing, Project administration, Methodology, Investigation, Data curation. **Michal Ferries:** Writing – review & editing, Methodology, Investigation, Data curation. **Barry Greenfield:** Writing – review & editing, Methodology, Investigation, Data curation. **Emily J. Douglas:** Writing – review & editing, Validation, Methodology, Investigation. **Reuben Hattingh:** Writing – review & editing, Methodology, Investigation, Data curation. **Tarn Drylie:** Writing – review & editing, Methodology, Investigation. **Becky Shanahan:** Writing – review & editing, Methodology, Investigation. **Andrew M. Lohrer:** Writing – review & editing, Writing – original draft, Validation, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Data availability statement

All the data used is presented in this article.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.nexres.2025.100726](https://doi.org/10.1016/j.nexres.2025.100726).

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