1. Response of macrofauna community structure and function to extreme weather events on the river-influence continental shelf
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Abstract

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1. Introduction

The continental shelves account for 9-13% of marine primary production, 30% of the organic carbon burial, and 59% of the organic carbon reminerlization despite constituting only 7.5% of the global seafloor area (Burdige, 2007; Hall, 2002; Jahnke, 2010; Jørgensen et al., 2022). As major conduits between the land and sea, rivers export considerable amounts of terrigenous sediments, organic matter, freshwater, and nutrients into the coastal ocean (Dagg et al., 2004; Geyer et al., 2004; McKee et al., 2004). Rivers annually export XXX sediments, XXX nitrogen, and XXX phosphate in the ocean (cit.). While XXX of terrestrial organic matter was exported from rivers, 70% of terrestrial organic matter were buried in deltaic, whereas the decomposition rates of terrestrial organic matter reaches more than 70% (cit.). It is their disproportional biogeochemical contribution and significant inputs from rivers that made the continental shelves in the river-dominated ocean margins (RiOMar, sensu McKee et al., 2004) unique and important in the global carbon cycle.

In the shelf benthic ecosystems, the macrofauna – operationally defined as animals retained on a 300 μm mesh sieve – constitute significant proportions of the seafloor biomass, exhibit high biodiversity, and facilitate multiple key ecosystem functions in the sediments (Snelgrove, 1999, 1998). Through sediment reworking and bioirrigation activities, macrofauna redistribute solutes and particles within the sediment column, stimulating microbial activities, organic matter decomposition, and nutrient cycling (Lohrer et al., 2004; Mermillod-Blondin and Rosenberg, 2006). The activities of macrofauna also increase sediment erodibility, intensifying sediment resuspension, which in turn alters the physical environment of the seabed (Hillman et al., 2020; Kristensen et al., 2013). Macrofauna are trophic links from the detrital pool to higher trophic levels, channeling energy from terrestrial- and marine-derived organic matter to the marine food webs (Darnaude et al., 2004; Dias et al., 2016). Despite their ecological significance, little integration among geological, chemical, and biological RiOMar studies leaving the ecological significance of macrofauna unclear (McKee et al. 2004).

Considering the processes that shapes the abundance and composition of RiOMar shelf benthic communities, Rhoads et al. (1985) proposed a conceptual model describing how the intrusion of sediments and nutrients from river floods affect the benthic communities in continental shelves. During flood events, substantial amounts of riverine sediments were deposited near the river mouth, which imposes strong physical stress on the benthic communities, leading to local extinction of the sediment communities. As water clarity improves with lower suspended sediment concentration, nutrient-enriched river plumes stimulate water primary production and enhance the phytodetritus availability on the seafloor, hence supporting benthic communities in greater abundance.

Empirical studies across the world echoed the conceptual model from Rhoads et al. (1985), confirming the role of river floods on shelf benthic community dynamics (Akoumianaki et al., 2013; Aller and Stupakoff, 1996; Alongi et al., 1992; Bonifácio et al., 2014; Wheatcroft, 2006). Mass sediment deposition during peak river discharge imposed significant physical stress on the shelf benthos, eradicating taxa intolerant to rapid sediment accumulation (Akoumianaki et al., 2013; Aller and Aller, 1986; Alongi et al., 1992; Bonifácio et al., 2014). Reduction of average body size (Aller and Aller, 1986), alteration of community size structure (Akoumianaki et al., 2006; Wheatcroft, 2006), and compositional change (Akoumianaki et al., 2013; Aller and Stupakoff, 1996; Bonifácio et al., 2014) of the shelf macrobenthos were reported after flood events. These adverse effects of intense sedimentation were relieved away from the river mouth, resulting in greater abundance and diversity of the benthic macrofauna (Akoumianaki et al., 2013; Aller and Stupakoff, 1996; Alongi et al., 1992; Bonifácio et al., 2014). Positive correlation between pelagic primary production and macrofaunal abundance along the river-sea gradient further indicated the subsidization of phytodetritus to the benthic communities (Alongi and Robertson, 1995).

While many studies documented the changes in benthic communities before, during, and after floods, few studies have explored the associated changes on the fauna-mediated seafloor ecosystem function, leaving uncertainty in how flood events. Through the lens of disturbance ecology, river floods are pulse events that not only reduce community biomasses but also supply the communities with resources (Jentsch and White, 2019). Field experiments of flood sedimentation found that defaunation occurred regardless of sedimentation intensity (cit.). Benthic communities in sandy and muddy sediments have varying tolerance to sedimentation (cit.). Incubation experiments analyzing the causation between the benthic community and the oxygen consumption further revealed that defaunatation were associated with the decrease of sediment oxygen consumption after an artificial sedimentation event (Mestdagh et al., 2018). Although, little information was shown to disentangle. Correlational studies revealed positive relationships between river floods and macrofauna abundance (cit.). As the intensity of extreme precipitation events (tropical cyclones, storms) are expected to intensify (cit.), it is crucial to document the benthic response to extreme sedimentation events to project ecosystem stability in the changing climate.

At the western Pacific, the arc-continent collision of the Eurasia plate and the Philippine Sea plate exhumed the Taiwan island (Teng, 1990), and spawned several small mountainous rivers (SMR) around the island’s mountain belts. These SMRs, despite of their small drainage sizes, export mass sediments comaparable to large rivers during extreme events, contributing greatly to global sediment budget (Kao and Milliman, 2008; Milliman and Syvitski, 1992). The Gaoping River, as the second longest river of Taiwan with a drainage area of 3,250 km2, annually discharges 36-49 Mt of sediment into the ocean (cit.). Extreme, episodic events such as typhoons and earthquakes contribute greatly to the river’s annual sediment discharge, exporting sediments comparable to the river’s annual flux within days (e.g., 48 Mt during Typhoon Herb, Milliman & Kao 2005). The event-driven floods with high concentrations of sediments would then fed into the Gaoping Submarine Canyon, efficiently transporting the sediments to the deep sea (Liu et al. 2012). On the other hand, the continental shelf and slope seafloor will be covered with flood sediments with thicknesses ranging 2-12 cm weeks after the typhoons (Huh et al. 2009a). The organic content of the seafloor reflects the sediment’s deposition pattern. More than XX% of the riverine POC were deposited in the Gaoping Submarine Canyon is enriched with organic matters, whereas the organic matter in the canyon is mainly terrestrial (cit.). Around 24% of the riverine POC was sequestrated into the shelf and slope sediments (Hsu et al. 2014). The remaining 76% of missing river POC were either degraded or exported further to the open waters (Hsu et al. 2014). Considering the episodic nature of sedimentation and organic matter input of the Gaoping River-Shelf system (GRS), the GRS is a great observation site to investigate how the interplay of episodic disturbance and food subsidy shapes the shelf benthic ecosystem adjacent to a SMR.

In this study, we conducted two research curises in 2019 before and after the wet season to measure changes in the macrobenthic community and the environment in the GRS. One typhoon named Typhoon Bailu made landfall on August 24th and caused significant damage to southern and eastern Taiwan (Lin et al., 2020). Within two days, the cumulative precipitation among the affected cities and counties ranged from 100 to 700 mm. 11 and 25 incidents of flood and landslides occurred, respectively. 6 people were injured, more than 100,000 households experienced a power outage, and 2,000 households experienced a water outage. The total agricultural production loss was estimated around 170 million NTD. Exported driftwoods from rivers filled up Fugang Fishing Harbor entirely, causing disturptions to local marine traffic. Despite the immense societal damage and economical loss, the typhoon provided a rare opportunity to examine the response of the benthic communities to river floods triggered by an extreme weather event. As river floods influence sediment discharge patterns and terrestrial organic carbon export, we hypothesize that physical disturbance and food subsidy are the main factors shaping benthic communities in the GRS. The episodic sediment discharge during flooding could exert pulse-type disturbances onto the marine communities. The present study analyzed the change of macrofaunal abundance, biomass, composition, and the sediment community oxygen consumption (SCOC) to compare the benthic community structure and ecosystem functions before and after the impact of the typhoon flood. We further identified environmental variables that potentially control the macrofaunal abundance, biomass, composition, and respiration on the river-influenced continental shelf benthic ecosystem.

1. Material and methods
   1. Shipboard sampling

Two research cruises were conducted by R/V Ocean Researcher 1 (OR1; operated by National Taiwan University) to collect biological and geochemical data in the Gaoping Continental Shelf (GS) in March (OR1-1219) and October 2019 (OR1-1242) (Fig. 1). Station S4 was only visited in March, while Stations S1 and S2 were visited in October. Stations S3, S5, S6, and S7 were visited on both cruises.

In each station, Conductivity-Temperature-Depth (CTD) sensors were deployed to collect the profiles of salinity, temperature, light transmission, fluorescence, and dissolved oxygen from the surface water to 5 m above the seafloor. The rosette bottles on the CTD also collected bottom water for sediment incubation. Multi-corers were deployed to collect sediment. Two core tubes were sectioned into 1-cm slices from top to bottom for analyzing geochemical signatures, such as sediment grain size, sediment porosity, and other bulk sediment compounds. Another three core tubes with longer sediment lengths and better integrity were chosen for shipboard incubation (Glud, 2008).

The three sediment cores were incubated in a temperature-controlled water bath under dark condition to measure the total oxygen utilization (TOU) of the sediment. The water bath temperature was set to be within the range of the bottom water temperatures measured with CTD. Each sediment core was sealed by a plastic lid with a magnetic stir bar attached inside. After removing the air bubbles in the overlying water, another magnet attached to a motor was placed above the plastic lid, coupling to the stir bar underneath. Both motor and magnet bars rotated and stirred the overlying water at 60 rpm to prevent water stratification. Every four 4 to 6 hours, we used a miniature oxygen optode (PreSens PSt7) to measure oxygen concentration through a small resealable sampling port and a temperature sensor (PreSens Pt100) for the water bath temperature. The oxygen optode was calibrated for each cruise by scanning the product-specific barcode. We used PreSens Microx 4 data logger to record the dissolved oxygen and temperature until the oxygen levels dropped below 85% of the initial concentration (Glud, 2008). We then used the following equation to estimate TOU (Song et al., 2016):

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where m is the regression slope, V is water volume, A is sediment area, and 24/1000 is a constant that adjusts TOU’s unit to mmol m-2 d-1. The TOU measurements were adjusted to *in situ* values using the temperature coefficient Q10 (Valiela, 2015).

Q10 was assumed to be 2, as for most ectotherms; Rincub. and Tincub. were the measured oxygen utilization and incubated temperature; and Tin situ was bottom water temperature. After sediment incubation, the upper 10 cm of the sediment was sieved through a 300 um mesh sieve and washed with filtered seawater to retain macrofauna. The retained samples were then fixed with a 1:1 ratio of filtered seawater and a Rose Bengal-stained 10% formaldehyde solution. The samples were fixed and stained for at least a week before being transferred to 70% ethanol for preservation, sorting, and measuring for body size.

* 1. Laboratory analysis

Median grain size (D50), sand fraction, silt fraction, and clay fractions were measured with a laser diffraction size analyzer (Model LS-13320; Beckman Coulter Inc.). Sediment porosity (Por) and water content were measured by calculating the volume and weight difference after 100℃ for 24 hours, assuming a specific density of 1.024 g cm-3 (Blum, 1997).

To measure total organic carbon (TOC) and stable isotopic carbon (δ13C) the sediment subsamples were first acidified with 6N HCL and then sent to the Flash 2000 elemental analyzer in tandem with a GC-Isolink interface to a Delta V Plus isotope ratio mass spectrometer (both from Thermo Fisher Scientific). TOC values were reported in percent weight contribution, while δ13C values were calculated using Vienna-PeeDee Belemnite as the reference point and reported in ‰ differences. Total nitrogen (TN) measurements were similar to TOC and δ13C, except no acid pretreatments were applied before sending the sediment samples into the same instruments. TOC were then divided with TN to calculate carbon-to-nitrogen ratio (C/N ratio). For sediment chlorophyll a (Chla), the sediment samples were first immersed in 10-ml acetone-water solution with a volumetric ratio of 9:1 in the dark at 4℃ for 24 hours. The chlorophyll extracts were then measured with a fluorometer (Model 10-AU; Turner Designs, Inc.) and reported in nanogram per gram dry weight. Only the environmental data from the top 0-1 cm of the sediment were included for later analyses.

Fauna samples were sorted into major taxa (mostly at order level) and measured the length and width with an ocular micrometer for biomass estimation. The abundance was estimated by the specimens with intact cephalic region. The biovolumes were calculated using the Length-Width Relationship (LWR):

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where V is the individual volume; c is the taxon-specific conversion factor; L and W are the maximum length and width of the individual (Feller and Warwick, 1988). The taxa without conversion factors used those from taxa with similar body shapes. The biovolumes of xxx, xxx, and xxx were estimated by geometric shapes (i.e., cylinder, cone, ellipsoid) (e.g., Hillebrand et al. 1999, Benoist et al., 2019). The derived biovolumes were then converted to wet weight by assuming a specific density of 1.13 (Gerlach et al., 1985).

* 1. Data analysis

The response variables, including relative abundance and biomass of macrofauna taxa, were Box-Cox-chord transformed to reduce the data skewness and make the resulting distance matrix double-zero asymmetrical (Legendre and Borcard, 2018). Box-Cox-chord transformation provides a series of exponents for ecologists to control the data symmetry. For example, the Box-Cox-chord transformation with exponents of 0.5, 0.25, and 0 are equivalent to the square root, fourth root, and log-transformed frequencies. In this study, the best exponents, 0.3 and 0.1, were identified by the Dagnelie test of multi-normality for abundance and biomass compositional data, respectively (Legendre and Borcard, 2018). The transformed data was then subjected to Euclidean distance and principal component analysis (PCA) to visualize compositional differences between samples. Taxa with the highest loading on the first two PCs (> 0.4) were shown as vectors on the PCA plot. The total macrofauna abundance and biomass were log10 transformed before univariate analyses.

We divided explanatory variables into (1) spatiotemporal factors, including sampling time, water depth, and distance to river month, and (2) environmental variables of sediment geochemistry and bottomwater hydrography. The distance to the Gaoping River mouth (DRM) was calculated using the World Geodetic System 1984. The coordinate of the river mouth was set at 120.42⁰E and 22.47⁰N (figure 1). Environmental variables were subject to Dunn’s test seasonal variations across the Gaoping Continental Shelf (supp. Table). Highly correlated environmental variables (|r| > 0.7, Pearson correlation) were screened by ecological reasoning (Dormann et al., 2013). For example, coastal hypoxia (<63 μM) alters benthic benthic community stucture and function (Middelburg and Levin, 2009). Since all stations in this study were well-oxygenated (Fig. 2), the dissolved oxygen was excluded from analyses. Strong correlations were present between salinity, light transmission, and temperature (|r| > 0.7). Among them, temperature (Temp) was selected due to its overall control on biological processes (Brown et al., 2004). Clay, silt, sand fractions, and D50 were highly correlated (|r| > 0.7), and thus D50 was selected as the sole indicator of sediment granulometry. Porosity and TN were highly correlated (r > 0.7); however, TN was excluded since other geochemical indicators, such as CN ratio and Chla, also indicate organic matter quality (Campanyà-Llovet et al., 2017). δ13C and Chla were negatively correlated (r = -0.76). Nevertheless, Chla was included since δ13C signatures may be confounded by marine autochthonous carbon, modern terrestrial carbon, and petrogenic carbon in the present study area (Carter et al., 2012; Kao et al., 2006, also see discussion). The resulting variables, Temp, Fluo, Por, D50, TOC, CN, and Chla were centered and scaled to unit variance. Principal component analysis (PCA) was used to visualize the environmental variation among sampling sites.

Spatialtemporal variables, including water depth, DRM, and sampling time, were used to model macrofauna (1) composition, (2) total abundance, (3) total biomass, and (4) sediment total oxygen utilization (TOU). We used PERMANOVA with 9999 permutations on macrofauna compositions (Anderson, 2017) and fitted simple linear regressions on macrofauna total abundance, biomass, and TOU under multi-model inference. The multi-model framework uses information theory to account for uncertainty across several models, identifies competing models, and then draws inferences to avoid arbitrarily selecting a single model for inference (Burnham and Anderson, 2002). In short, we sought all possible combinations of the explanatory variables. Then, we reported an average model (Burnham and Anderson, 2002) from an un-nested top model set without a notable decrease in Akain Information Criteria for small sample size (ΔAICc < 6) (Richards, 2008, 2005).

Environmental variables were fitted to macrofauna composition, total abundance, total biomass, and TOU to identify potential drivers. Redundancy analysis (RDA) with backward selection was used to retain environmental variables best-described macrofauna composition. The taxa with the highest loading on the first two RDA axes (> 0.4) were shown as vectors on the RDA plot. Macrofauna total abundance, total biomass, and TOU were modeled by environmental variables with simple linear regression under a multi-model framework.

All data analyses were conducted using R version 4.0.3 (R Core Team, 2020) with additional statistical packages *vegan* (Oksanen et al., 2021), *MuMIn* (Bartoń, 2022). Packages *dplyr* and *tidyr* were used for data cleaning (Wickham, 2021; Wickham et al., 2021). Results were visualized with *ggplot2* and its extensions (Schloerke et al., 2021; Slowikowski, 2021; Wickham, 2016). P values are reported following the language of evidence (Muff et al., 2022). For example, P values ≥ 0.0001 and < 0.001 provide very strong evidence. P values ≥ 0.001 and < 0.01 indicate strong evidence. P values ≥ 0.01 and < 0.05, ≥ 0.05 and < 0.1, and ≥ 0.1 and < 1 suggest moderate, weak, and no evidence, respectively. Data and R code for reproducing the analyses are available at https://github.com/chenyenting1998/GRSmacrofauna.

1. Results
   1. Environmental condition and macrofauna

CTD profiles showed notable temporal variations (figure 2). Temperature, salinity, density, dissolved oxygen, and fluorescence profiles in March showed little vertical variation across stations. In contrast, temperature, salinity, and density, profiles in October were more stratified, with warm, brackish, light water occupying the upper water column and cold, saline, heavy water at the lower water column. Light transmission profiles during both cruises varied through the water column; however, the variations in October were more significant.

The PC1 and PC1 of the selected environmental variables explained 36.6 and 25.6% of the total variation (figure 3). *Temp*, *Fluo*, *Chla*, and *CN* significantly contributed to PC1, while *TOC*, *Por*, and *D50* had higher loading on PC2. The environmental conditions of the shallow stations (i.e., depth < 50 m; S2, S3, S6, and S7) were dissimilar between the two sampling periods. Higher CN, Chla, and D50 characterized the March sampling, whereas the October sampling observed higher Por, Fluo, and Temp. The environment of the deep sites (i.e., depth > 80 m; S1 and S5) in October was more similar to the shallow (i.e., depth < 50 m; S3, S6, and S7) than to the respective deep sites (i.e., depth > 80 m; S4 and S5) in March.

* 1. Macrofauna assemblage

We found 27 taxa belonging to phylums of Annelida, Arthopoda, Cnidaria, Echinodermata, Mollusca, Nematoda, Nemertea, Phoronida, Platyhelminthes, and Vertabrata. Across all 27 taxa, polychaetes dominated macrofauna abundance across all stations, contributing xx-xx% in March and xx-xx% in October (figure 4a). Amphipods and nematodes also contributed significantly to macrofauna abundance, accounting for xx-xx% and xx-xx% in March and xx-xx% and xx-xx% in October, respectively. In terms of biomass, polychaetes accounted for xx% of the total in S3 in March but less than xx% in the remaining stations further away from the river mouth (figure 4b). The biomass of these stations was dominated by ophiuroids (xx-xx%) instead. In October, polychaete biomass not only dominated S3 (xx%) but also became dominated in S5 and S6 (xx-xx%) and a new, deeper station, S1 (xx%). Between March and October, the ophiuroids’ contribution declined considerably in S5, S6 and S7. The decapod biomass seems to start to take over the ophiuroid biomass, becoming the most dominant group in S2 and S7 (xx-xx%) and the second most dominant group in S6 (xx%).

PERMANOVA tests revealed notable spatiotemporal variations in macrofauna abundance and biomass compositions (Table 1). For abundance composition, we found very strong depth (p = 0.0001) and DRM effects (p =0.0002), as well as moderate cruise effect (p = 0.046) and DRM-cruise interactions (p = 0.04). There were weak depth-DRM interactions (p = 0.08) and lack of evidence for depth-cruise interactions (p = 0.69). For biomass composition, we found very strong depth (p = 0.0001), strong DRM (p = 0.009), moderate cruise effects (p = 0.02), strong DRM-cruise interactions (p = 0.001), and no evidence of depth-cruise (p = 0.8016) and depth-DRM interactions (p = 0.251).

Principle component analyses generally agreed with the PERMANOVA results, revealing spatiotemporal variations in assemblage composition (figure 5). The PC1 and PC2 explained 18.1% and 15.9% of the total variation in macrofauna abundance composition, respectively (figure 5a). Peracarids (i.e., isopods, tanaids, and amphipods), aplacophorans, and hydroids had the highest loading on the first two PCs. The March samples were mostly characterized by high contributions of aplacophorans, tanids, and amphipods, while the October samples from shallower sites (S2, S3, S6, S7) were not. In terms of the macrofauna biomass composition, PC1 and PC2 explained 20.6% and 13.7% of the total variation (figure 5b). Aplacophorans, mysids, ophiuroids, and decapods had the highest loading on the first two PCs. High contributions of ophiuroids characterized many March sites and the deeper October sites (S1, S5). The shallower March sites (i.e., S2, S6, and S7) were characterized by high decopod contributions.

RDA analyses showed that the environmental drivers were similar between macrofauna abundance and biomass compositions (figure 6). The RDA1 and RDA2 explained xx% and xx% of the total variation in the abundance composition, respectively (figure 6a). *D50*, *Por*, *Chla*, *TOC*, and *CN* were retained in the final RDA model. Oligochaetes, mysids, and aplacophorans had the highest loading on the first two RDA axes. In terms of the biomass composition, RDA1 and RDA2 explained xx% and xx% of the total variance, respectively (figure 6b). *D50*, *Temp, Por*, *Chla*, *TOC*, and *CN* were retained in the final RDA model. Decapods, mysids, and aplacophorans had the highest loading on the first two RDA axes. The two RDAs agreed that *TOC*, *CN*, and *Chla* were the main environmental variables that drove the assemblage differences between the March (Stations S4, S5, S6, and S7) and October sampling. On the other hand, S1 and S3 of OR1-1242 were distinct from the organic matter gradient. S1 of OR1-1242 was characterized with high *D50*. S3 in OR1-1242 was characterized with high *Por* and mysid contributions. The main difference between the two RDAs is that the biomass RDA specifically showed in influence of *Temp* on the shallower OR1-1242 sites (S2, S3, S6, S7).

* 1. Macrofauna abundance, biomass, and TOU

The average macrofauna abundance across all samples was 8,966 ± 4,144 ind. m-2, with S7 in October having the lowest abundance of 4,626 ± 265 ind. m-2 andS3 in March having the highest abundance of 19,480 ± 1,836 ind. m-2 (figure 7). On the other hand, the average biomass. The average TOU was 15.6 ± 7.4 mmol O2 m-2 d-1, with S5 in March having the lowest TOU of 7.8 ± 0.9 mmol O2 m-2 d-1 and S3 in October having the highest TOU of 29.2 ± 2.3 mmol O2 m-2 d-1.

Macrofauna abundance, biomass, and sediment TOU showed strong spatiotemporal variations (table 2). For example, there was a very strong cruise effect (β = -0.24, p < 0.0001), DRM effect (β = -0.1512, p = 0.0001), cruise-DRM interaction (β = 0.16, p = 0.0001), strong cruise-depth interaction (β = 0.12, p = 0.004), moderate depth-DRM interaction (β = 0.06, p = 0.027), and weak depth effect (β = -0.06, p = 0.055) on the macrofauna abundance. We also found a very strong cruise-DRM interaction (β = 0.74, p = 0.0007), moderate DRM effect (β = -0.34, p = 0.048), but no evidence of cruise effect on the macrofauna biomass (β = 0.17, p = 0.405). In terms of the sediment TOU, there was a strong cruise effect (β = 4.48, p = 0.014), DRM effect (β = -2.38, p = 0.02), cruise-depth interactions (β = -4.28, p = 0.039), but no evidence of depth effect (β = -2.56, p = 0.157). The model average results generally echoed the scatterplot, showing apparent interactions between cruise and DRM on macrofauna abundance and biomass (figure 7a) and between cruise and depth on thee sediment TOU (figure 7b).

Model averaging results revealed seafloor environmental drivers for macrofauna abundance, biomass, and sediment TOU (table 3). For example, *CN* (β = 0.11, p < 0.0001), *D50* (β = -0.07, p = 0.0001), and *TOC* (β = 0.21, p < 0.0001) had very strong positive, negative, and positive effects on the macrofauna abundance, respectively. *Por* (β = -0.15, p = 0.002) and *Temp* (β = 0.07, p = 0.007) had strong negative and positive effects, and *Chla* (β = -0.07, p = 0.033) had a moderate negative effect on the macrofauna abundance. On the other hand, *Chla* (β = -0.92, p = 0.006), *CN* (β = -0.81, p = 0.004), and *Temp* (β = 0.52, p = 0.009) had strong negative or positive effects on the macrofauna biomass. *D50* (β = 0.39, p = 0.025) and *TOC* (β = 1.72, p = 0.027) had moderate positive, *Por* (β = -1.64, p = 0.011) had moderate negative, and *Fluo* (β = -0.20, p = 0.093) had weak negative effects on the biomass. For the sediment TOU, there were very strong positive Temp (β = 5.69, p < 0.0001), CN (β = 8.22, p < 0.0001), and Por (β = 14.8, p < 0.0001), negative TOC (β = -17.48, p < 0.0001) and D50 (β = -4.03, p = 0.0005), and negative *Chla* (β = 6.84, p = 0.0005) effects.

1. Discussion
   1. Study limitation

The measured DOU in the present study might not be representative to *in situ* conditions. DOU measurements in the Gaoping Continental Shelf were lower than the Rhone River delta (cit.), and other deltaic regions. *In situ* DOU measurements off the Rhone river have shown that sediment resuspension events could increase DOU to the factor of 2 within an hour; DOU would then 36 hours to return to its stabilizing state (Toussaint et al., 2014). Since the Gaoping Continental Shelf seafloor receives inputs from the Gaoping River and is subjected to tidal waves (Liu et al., 2002), it was likely that DOU can be as dynamic as in the Rhone river deltaic sediments. In fact, bottom water transmission dips in OR1-1242 indicated possible sediment resuspension events at the shelf seabed (figure 2). Also, oxygen profile measurements in the present study were done after sediment incubation, which generally took more than 24 hours, giving DOU enough time to drop back to the normal state. We therefore speculate that the DOU measured in the present study is systematically lower than those *in situ*. We warn that incubation experiments might stabilize the sediment, lowering the measured DOU, yielding erroneously high BOUs as a result. Also, future studies should specify when their oxygen profiles were measured.

* 1. Physical environment
* Porosity
  + Porosity had a strong negative effect on macrofauna abundance and biomass (table 3).
  + Eel River Continental Shelf was reported to have significant reduction of macrofauna abundance after flood deposits (Wheatcroft, 2006).
* Temperature
  + Strong correlations between temperature, salinity, density, and transmission.
  + While CTD profiles suggested that OR1-1219 was well-mixed, the profiles showed strong water stratification in OR1-1242 ().
* D50 in S1
  1. Organic matter indicators
* Chla and δ13C were negatively correlated (r = -0.76).
* Similarly, Akoumianaki et al. (2013) reported a weaker fit between biological and environmental data during flood season.
* Although greater quality and quantity of organic matter nurtures the seafloor biota (Campanyà-Llovet et al., 2017), the increase of organic matter quality and quantity more or less indicated the sedimentary condition of the seafloor.
* With a lifespan ranging months to years, the change of macrofauna in the present study xxxxxx.

1. Conclusions
2. Acknowledgements
3. References

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