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

* Role of sediment metazoans

On continental shelves, macrobenthos (organisms larger than 0.5 mm) are the ubiquitous and diverse faunal groups on the seafloor that facilitates several essential ecological functions at the sediment-water interface (Snelgrove 1998). Macrofauna abundance and distribution are shaped by abiotic factors such as light availability, hydrodynamic regime, sediment granulometry, and food availability, and biotic factors, including larva supply, competition, and predation (Gray 1974, Wilson 1990, Snelgrove & Butman 1995). Macrofauna activities, such as bioturbation, bioirrigation and filter-feeding may increase water transparency, facilitate sediment deposition and nutrient recycling, alter sediment stability, and sequestrate anthropogenic pollutants (Meysman et al. 2006, Mermillod-Blondin 2011, Hillman et al. 2020, Coppock et al. 2021). Macrofauna is also an important food source for consumers from higher trophic levels and may be commercially exploited (De Vlas 1979, Volvenko et al. 2020). Despite the considerable ecological functioning, the ongoing change in the marine environment has disturbed the natural biological dynamics of marine macrofauna. With the ongoing climate change, elucidating the interactions between marine benthos and the environment under extreme weather event is vital to project future conditions of seafloor functioning and provide management applications (Bianchi et al., 2021).

* Effects of physical disturbance

Harris (2014) classified a variety of marine physical disturbances that could perturb the seafloor biota into two regimes, including pulse-type disturbances and press-type disturbances. The pulse-type disturbances, such as tropical storms, refer to short-term, intense disturbances that could immediately overturn the marine benthos. The press-type disturbances, such as waves and tides, are moderate physical stresses that could sustain for prolonged periods, removing the benthos eventually. Rhoads et al. (1985) proposed a conceptual model arguing that the benthic community patterns at the river-dominated continental shelf are shaped by sedimentation stress and food supply along the land-sea gradient. In brief, episodic flood events of the river would discharge mass sediments and effluents into the coastal waters, causing intense sedimentation near the river mouth. The deposition of mass sediments would then cause local extinctions of the sediment fauna near the river mouth, suppressing the benthic standing stock and their ecological functioning in the sedimentary environment. As further away from the river mouth, improved water clarity and still abundant nutrients from the river would stimulate primary production in the water column, increasing the phytodetritus flux to the seafloor. The benthic communities could then thrive on the increased food supply and decreased sedimentation, resulting in higher benthic standing stocks and greater material fluxes at the sediment water interface. However, the benthic standing stock and biological activity would reduce further offshore due to declining nutrients and food supply in the open waters.

Empirical studies conducted across the world generally echoed Rhoads et al. (1985), suggesting that the sedimentation from river runoff shapes the spatial pattern of benthic communities (cite all studies that reported sedimentation stress). During peak discharge, the macrofauna standing stocks and diversity decreased near the river mouth (Aller & Aller 1986, Alongi et al. 1992, Wheatcroft 2006), with the taxonomic composition dominated by mobile subsurface deposit feeders and carnivores (Aller & Aller 1986, Akoumianaki et al. 2013). The mean body size was smaller, and the size structure was more variable near the river mouth and under high sedimentation stress (Aller & Aller 1986, Alongi et al. 1992, Aller & Stupakoff 1996, Akoumianaki et al. 2006). These adverse influences of river discharges were relieved away from the river, resulting in greater abundance and diversity and likely altering the functional composition and size structure of the benthic macrofauna (Rhoads et al. 1985, Aller & Aller 1986, Akoumianaki et al. 2006, Hermand et al. 2008). In regard to local climate, trade winds can also , confounding the impact of riverine impact on the shelf bnethos. In the long term, the community structure in the river-influenced continenthal shelves may be unpredictable (Salen-Picard polychaete paper).

Although Rhoads et al. (1985) did not explicitly describe the patterns of macrofauna community succession, studies on the continental shelves off the Amazon River, the Spercheios River, and the Rhône River could provide some evidence on the temporal dynamics. On the Amazon River shelf, seasonal variation in river runoff and wind stress imposed significant physical stress onto the benthic comminuty, controlling the standing stock, size structure, diversity, functional composition, recruitment, and behavior of the sediment macrofauna (Aller & Stupakoff 1996). The macrofauna standing stock decreased during high river runoff and strong trade winds. The body size was generally below 1 mm and dominated by deposit-feeding and carnivorous species. The remaining macrofauna was larger but still below 5 cm. During low river runoff and weak trade wind, the macrofauna recruits recolonized the seafloor. They grew to larger sizes with deeper burrows and higher overall standing stock, and their recovery proceeded until the onset of the subsequent high river runoff and high wind stress. On the Spercheios River shelf, Greece, macrofauna density increased with the distance from the river during the high runoff but decreased during the low runoff. In contrast, the macrofauna species richness decreased with the distance from the river regardless of the high or low runoff conditions (Akoumianaki et al., 2013). The macrofauna composition strongly correlated to food supply and sediment characteristics during low river runoffs; however, such a relationship weakened during peak river runoff (Akoumianaki et al., 2013). Near the Rhône River, the macrofauna density and diversity decreased after flood events due to the intense sedimentation; however, the density and diversity then increased more than 2-fold during the dry season, suggesting a community recovery from sedimentation stress. However, such temporal dynamics in community density and diversity were not evident further away from the Rhône River. Based on evidence from these three river-influenced shelves, the macrofauna communities near the river mouth were more dynamic than those further offshore. The communities responded negatively to sedimentation during peak river discharge and re-established themselves during low river runoff. These observations highlight the spatiotemporal variations of riverine influence on the marine macrofauna.

* Study area (extract thesis text)

Located on the east side of the northern South China Sea (nSCS), the Gaoping river-shelf (GRS) comprises the Gaoping River and Gaoping shelf. The Gaoping River is a small mountainous river (SMR) and the second-longest river in Taiwan. The drainage area of the Gaoping River is 3,250 km2 with annual sediment discharged ~36-49 Mt, equivalent to a sediment yield of 11,000 t km2 yr-1 (Milliman & Syvitski 1992, Liu et al. 2009). The Gaoping shelf is a narrow shelf with a length of 100 km and a width of 20 km (Yu & Chiang 1997). The Gaoping Shelf can be further separated into northern and southern lobes by the incision of the Gaoping Submarine canyon at the vicinity of the Gaoping River mouth (Yu & Chiang 1997). The rainfall patterns of the Taiwan orogen receive strong influences from seasonal monsoons and typhoons, demonstrating distinct dry and wet seasonal precipitation patterns (Chen et al. 2010, Liu et al. 2016a, Water Resource Agency 2020). On average, 89% of southern Taiwan’s annual precipitation occurs during the wet season (May-October, Water Resource Agency 2020). As the largest river in south Taiwan, the Gaoping River, on average, exports 78% of its annual water discharge from June to September (Liu et al. 2002). The sediment discharge of the Gaoping River during the wet season is also two to three orders of magnitude larger than those during the dry season (Hung et al. 2004; cited in Liu et al. 2016). Typhoons frequently visit Taiwan during the wet season (~4 per year; Liu et al. 2013) and bring significant precipitation, accounting for 47.5% of the total annual rainfall (Chen et al. 2010). The typhoon-driven floods in the Gaoping River export large quantities of sediment comparable to the annual sediment load in a matter of days, hence playing a significant role in sediment transport (Liu et al. 2013). For instance, the Gaoping River exported 48 Mt of sediments within three days during the passing of typhoon Herb in 1996 (Milliman & Kao 2005). Such a high sediment load within a short period is comparable to its annual sediment flux (49 Mt; Liu et al. 2009), highlighting the event-driven sediment discharge pattern of SMRs. The typhoon-driven floods also bear high concentrations of suspended sediments (> 40 g L-1; Milliman & Kao 2005), initiating hyperpycnal flows that plunge the sediments into the Gaoping Submarine Canyon (Liu et al. 2012). In addition, suspended sediments carried by the typhoon-driven floods would gradually settle on the shelf and slope seafloor, forming flood sediment layers with thicknesses ranging 2-12 cm weeks after the typhoons (Huh et al. 2009a).

Regarding the particulate organic carbon (POC) flux, the Gaoping river transports 5.98 X 106 g C d-1 in the dry seasons and 1.25 to 276 X 107 g C d-1 in the wet seasons (Hung et al. 2012). Modern terrestrial carbon composes around 30% of the riverine POC, while fossil carbon contributes the remaining 70% (Kao et al. 2014). Furthermore, the amount of modern carbon export correlates well with the magnitude of water discharge, indicating a hydrological control on the terrestrial POC export (Kao et al. 2014). Under normal water discharge conditions, dispersive hypopycnal plumes (i.e., lighter than seawater) carry and spread the terrestrial organic matter all over the shelf seafloor. The seafloor sediments contain a mixture of riverine and marine carbon signals (Kao et al. 2006, 2014). By contrast, flood events mobilize massive terrestrial deposits, triggering hyperpycnal plumes (i.e., heavier than seawater) that transport the sediments and the riverine POCs directly into the Gaoping submarine canyon, eventually delivered to the deep sea (Kao et al. 2014, Sparkes et al. 2015, Liu et al. 2016a). Significant accumulation of modern carbon was also found in the shallow inner shelf after typhoons, suggesting that extreme river discharge is the prime mechanism for terrestrial biomass export into the deep sea and the shelf sediments (Sparkes et al. 2015). Despite the massive sediment influx from the Gaoping river, the modern carbon seemed restricted to the inner shelf and the canyon. The sediment flux further into the open margins was mainly contributed by hemipelagic sedimentation (Huh et al. 2009a, Zheng et al. 2017). Moreover, only ~24% of the river 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). Within the deposited fraction, less than 30% of the total terrestrial organic matter was lost (i.e., through remineralization) during transportation (Kao et al. 2014).

* Study objective

In this study, we conducted two separated research curises to sample macrobenthos and associated hydrographic and sedimentary environmental parameters in the Gaoping-river shelf (GRS) before and after Typhoon Bailu made landfall in the southern Taiwan on August 24th, 2019. The 2019 Typhoon Bailu brought extreme precipitation and caused flooding and landslides in southern Taiwan (Lin et al., 2020). The typhoon also severely damaged harbors, caused death, injuries, and agricultural production loss around 170 million NTD (Lin et al., 2020). Despite the immense damage Bailu had caused, the typhoon provided a rare opportunity to examine the response of the benthic communities to extreme weather events. As the extreme weather events may 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 employ a variety of community-level analyses such as macrofaunal abundance, biomass, composition, and the sediment community oxygen consumption (SCOC) to compare the benthic community structure and functions before and after the Typhoon impact. We further identify environmental variables that potentially control the faunal composition, abundance, biomass, and respiration on the river-influence continental shelf.

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 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 fixed samples were allowed to sit 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).

We measured total organic carbon (TOC), total nitrogen (TN), carbon-to-nitrogen ratio (CN), sediment chlorophyll a (Chla), and stable isotopic carbon (δ13C) of the surface sediments (approximately 0 - 1 cm). 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) to measure TOC and δ13C. 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. TN measurements were similar to TOC and δ13C, except no acid pretreatments were applied before sending the sediment samples into the same instruments. CN ratio was then derived by dividing TOC with TN. For 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.

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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