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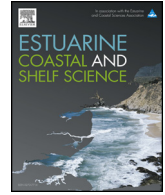
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# Recolonization of mollusc assemblages in mangrove plantations damaged by Typhoon Chan-hom in the Philippines

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## ABSTRACT

We investigated the effects of a catastrophic typhoon on mollusc assemblages of damaged mangrove plantations of different ages. Molluscs were sampled from infaunal, epifaunal and arboreal assemblages of mangrove stands in Lingayen Gulf, northwest Philippines, and compared with assemblages of un-impacted areas. Prior to the occurrence of the typhoon, there were clear shifts in the species diversity ( $H'$ ) and composition of mollusc assemblages with stand age of mangrove forests. This was observed in species composition through the succession in dominance from pioneer to seral or putative climax species, and assemblage type (as arboreal, epifaunal and infaunal). However, severe damage to vegetation structure and sediment properties (associated with a reduction in tree density and canopy cover resulting in increased temperatures and exposure) following the typhoon resulted in an alteration of trajectory patterns in the damaged stands. There were shifts in species composition and dominant species from having mature mangrove-associated species (pre-typhoon) to an abrupt return in dominance of pioneer species (post-typhoon). The damage was more evident in older stands than in intermediate-aged stands. Furthermore, the reduced presence of molluscs (and also probably their activities, i.e. burrowing) may have contributed to the delayed recovery of mangroves. The prospects for recovery of the system to pre-typhoon levels are therefore uncertain where the re-establishment of seral or edaphic mollusc assemblages appears to be related to the recovery of vegetation and sediment conditions.

## 1. Introduction

Mangrove restoration (mainly through plantation) has been a popular resource management program in the Philippines since the late 1980s (Salmo et al., 2007). Mangrove planting has been widely practiced in most parts of the country and gains community support because of the employment that it provides to locals. Aside from the main objectives of restoring forest cover and providing protection from typhoons, mangrove planting is also used to enhance coastal fisheries production. Among fisheries products expected to be derived from mangrove plantations are nekton (especially fishes, crabs and shrimps) and molluscs (Salmo et al., 2018).

Upon growth of replanted mangroves, their forest structure becomes more complex, and increasing amounts of detritus are produced, providing food and habitat for various organisms (see reviews by Cannicci et al., 2008; Nagelkerken et al., 2008). Patterns of changes in the density, biomass and species composition of the fauna are expected to occur as the forest vegetation changes with stand age. Among

mangrove-associated faunal groups, molluscs are one of the more conspicuous organisms. Changes in the mangrove community will likely influence shifts in species composition, abundance, and biomass of the mollusc assemblage (Sasekumar and Chong, 1998; Netto and Galucci, 2003) and will vary with assemblage types (from infauna to epifauna and arboreal). We adapted the definitions of assemblage types as infauna (molluscs inside the sediment), epifauna (molluscs on the sediment surface), and arboreal (molluscs attached to the mangrove stems and prop roots; cf. Salmo et al., 2017). Other factors that are known to affect the distribution and composition of benthic fauna (e.g., physical attachment, structural complexity, tidal elevation) have been assessed in several studies (see Kathiresan and Bingham, 2001; Chapman and Tolhurst, 2007; Nagelkerken et al., 2008 *inter alia*). The role of forest cover in mollusc abundance and biomass has been emphasized by Fondo and Martens (1998) and Sasekumar and Chong (1998).

This notable dependence of mollusc fauna on habitat condition leaves them vulnerable to severe disturbance events like typhoons.

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Typhoons are natural disturbances that frequently occur especially in the tropics. In the Philippines, around 20 typhoons occur each year, with intense events ( $> 150 \text{ km h}^{-1}$ ) having 16–32 years oscillation (Kubota and Chan, 2009). The particularly severe typhoons bring strong winds, intense rainfall and large storm surges causing notable damages to the environment, property and human lives, particularly in coastal areas (Cinco et al., 2016). These larger typhoons are known to cause significant reductions in mangrove forest cover as well as an associated loss of organic matter in sediments (Salmo et al., 2014). However, the extent and scale of damage within a forest stand are heterogeneous and vary with wind speed and localized site gradients such as geographical position relative to shoreline and tree height (Everham and Brokaw, 1996; Busby et al., 2008). Mangrove plantations are perceived to be more vulnerable than natural stands because of their lower structural complexity and lower wind firmness (cf. Gardiner and Quine, 2000).

There is an acknowledged need to investigate the colonization by molluscs in mangrove forests damaged by typhoons. Prior to the typhoon, we reported a clear trajectory of mollusc colonization and shift of dominant species as well as assemblage type (from arboreal to epifauna to infauna) with age of the stands (Salmo et al., 2017). Such shifts are correlated with the changes in vegetation and sediment conditions primarily with canopy cover and biomass (for the vegetation) and OM (in the sediments). Some species dominate in young plantations ( $< 10$  years; *Pirenella cingulata*) and in intermediate-aged plantations (10–15 years; *Nerita polita*), while other species are known to occur most in mature ( $> 15$  years) and natural stands (*Terebralia sulcata*; *Nerita planospira*). The species *P. cingulata* and *N. polita* dominates in infaunal and epifaunal assemblages while *T. sulcata* and *N. planospira* are more prominent in arboreal assemblage. Catastrophic typhoons are likely to contribute to reductions in habitat quality as well as a decrease in the supply of food for molluscs. An alteration of mollusc colonization pattern but more particularly a shift in dominant species (e.g. reverting from pre-typhoon mangrove-associated species to post-typhoon pioneer species in mature plantation) may commence after drastic changes in vegetation and sediment conditions. Smith et al. (1994) stressed however that the effects of such severe disturbances on the recruitment and colonization dynamics of mangrove-resident fauna had not been adequately studied.

When severe Typhoon Chan-hom struck Lingayen Gulf in northwestern Philippines on 9<sup>th</sup> May 2009 affecting our established study sites, we took the opportunity to test the hypothesis that mangrove habitat degradation caused by severe typhoons might influence and possibly disrupt the colonization and restoration of mollusc assemblages. The following account documents our subsequent findings on the effects of Typhoon Chan-hom on the recolonization of mangrove mollusc assemblages (from arboreal to epifaunal and infaunal assemblages) in mangrove plantations in the Philippines. Based on these new observations, we provide a re-evaluation of the possible role of molluscs in the post-disturbance recovery of mangrove habitat.

## 2. Materials and methods

### 2.1. Site description

The study was conducted in *Rhizophora mucronata* plantation stands of different ages in Lingayen Gulf, northwestern Philippines (Fig. 1). These plantation plots (codes in brackets) were: in Tondol, Anda (6 years – labelled as P6); Mona, Alaminos (8 years – P8); Imbo, Anda (10 years – P10); Pilar, Bolinao (11 years – P11); and Bangrin, Bani (18 years – P18). Mangrove plantations in Alaminos, Anda and Bolinao are more exposed to coastal processes, while those in Bani are located in sheltered areas in Tambac Bay and receive freshwater inputs from the Bani River. Mangrove plantations (dominated by *R. mucronata*) in the Central Philippines (Fig. 1) were also included: in Buswang, Kalibo, Panay Island (12 and 17 years – P12 and P17); and Banacon Island,

Getafe, Bohol (50 years – P50). Three natural mangrove forests (of unknown ages; neither planted nor obviously damaged) were used as reference sites (cf Cairns and Heckman, 1996; Ruiz-Jaen and Aide, 2005) to plot, estimate and compare the restoration trajectory of the restored mangroves relative to natural mangrove stands. These natural *R. mucronata* stands (Fig. 1) were in Buenavista in Bohol (Nx), central Philippines; and Masinloc (Ny) and Palauig (Nz) in Zambales, north-northwestern Philippines shown as Nx, Ny and Nz, respectively in Fig. 1. These forests are dominated (by at least 80%) notably by *R. mucronata* (with some *R. apiculata*, *R. stylosa*, *Avicennia marina* and *Sonneratia alba*). These mangrove sites are also protected by national environmental laws.

The tidal inundation varies widely and ranges from 1.30 to 1.50 m (Lingayen Gulf and Zambales) to 2.10–2.60 m (Bohol and Aklan; WXTide32; see [www.wxtide32.com](http://www.wxtide32.com), accessed 15 December 2016). All sites receive precipitation of more than 1700 mm year<sup>-1</sup>. Based on the modified Corona Classification system (Lantican, 2001), sites in Lingayen Gulf and Zambales have Type 1 climate (with two pronounced seasons, dry from November to April and wet from May to October), Aklan has Type II (no dry season, but a pronounced wet season from December to February), and Bohol has Type IV (no pronounced wet and dry seasons). Detailed information on vegetation and physico-chemical characteristics of each stand and site can be found in Salmo et al. (2013, 2014, 2017).

### 2.2. Typhoon Chan-hom (= Typhoon Emong)

Typhoon Chan-hom (known locally as Typhoon Emong) was the fifth typhoon that entered the Philippines in the 2009 season. Four other typhoons (Nangka, Ketsana, Parma and Miri-nae) crossed the Lingayen Gulf in that season; however, these typhoons had lower wind speeds and did not pass as close to the study sites (Fig. 1). Typhoon Chan-hom was formed near SE Vietnam in the West Philippine Sea and crossed the Philippine Area of Responsibility (PAR) on 3 May 2009. It had strong winds of 85–150 km h<sup>-1</sup> and was categorized as Typhoon 2 under the Saffir-Simpson Scale. Typhoon Chan-hom first crossed land at Cape Bolinao on 7 May 2009 (see typhoon path in Fig. 1) bringing with it strong winds, heavy rains (at least 200 mm in 24 h), and flooding which directly affected the mangroves in northwestern Lingayen Gulf. Plots P6, P8, P10, P11 and P18 were within ca. 5 km of the path of the typhoon (Fig. 1; Kitamoto, 2009). P12 and P17 were approximately 600 km from the path of the typhoon. Sites in Zambales were approximately 100 km from the typhoon path, while P50 and Nx were approximately 800 km from the path. Sites that were  $> 80$  km from the path were considered to be unaffected by the typhoon.

### 2.3. Sampling design

The effects of Typhoon Chan-hom on mollusc assemblages and in disrupting the pattern of restoration trajectory were evaluated. Mollusc sampling was carried out in the mangrove vegetation plots before the typhoon in December 2008 (pre-typhoon; see Salmo et al., 2017). Subsequent samplings were made at 0.5-mo and 7-mo post-typhoon in May and December 2009, respectively. Additional measurements were made for Lingayen Gulf sites at 9-mo post-typhoon (March 2010) to further establish the patterns of damage and regeneration in typhoon-impacted sites. Additional sampling was also carried out in natural mangrove sites in Zambales (Ny and Nz) at 9-mo post-typhoon to provide comparison with the mangrove plantations in Lingayen Gulf.

#### 2.3.1. Mollusc sampling

Mollusc sampling was carried out in the same vegetation plots we had used in previous studies ( $n =$  three plots per site; Salmo et al., 2013, 2014, 2017). Sampling was done during low tide. Each plot was of 5 m radius. Molluscs were collected and measured from three faunal components within the mangrove forest: arboreal (molluscs attached to

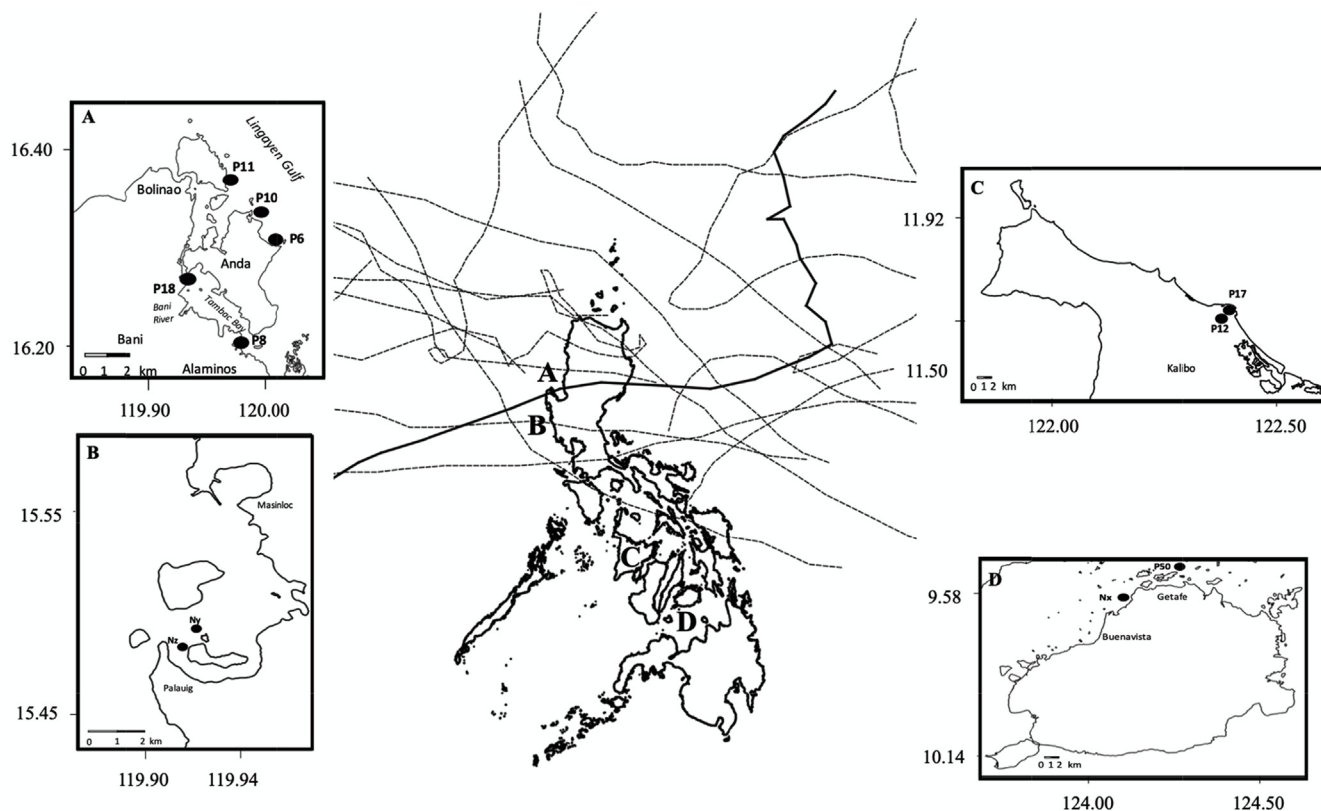


Fig. 1. Location of the study sites. Numbers indicate the age of plantation. P – planted mangroves, N – Natural mangroves. The dashed lines indicate the tropical weather disturbances that occurred in the Philippine Area of Responsibility (PAR) in 2009. The solid line corresponds to the path of Typhoon Chan-hom.

the mangrove stems and prop roots), epifaunal (molluscs collected from the sediment surface), and infaunal (molluscs collected from the top 10 cm of the sediment). For the arboreal component, molluscs were collected in the entire plot from the stems and roots of mangroves up to the highest points of the top-most prop roots (for the genus *Rhizophora*) and in the pneumatophores and up to 1.3 m height (above the substrate at low tide) for non-*Rhizophora* species. For epifauna, three 1 × 1 m quadrats were randomly established within each plot. All epifaunal individuals within the quadrat were collected via visual search. For infauna, three haphazardly located, replicate sediment cores were collected from each plot using a core sampler (diameter 6.5 cm) to 10 cm depth, packed in aluminum foil. The collected sediments were washed gently with water and passed through a 1 mm square mesh sieve. All collected mollusc specimens were brought to the laboratory for processing.

In the laboratory, all collected specimens were washed, dried and weighed and preserved in 70 % alcohol until identification. The specimens were identified with reference to Dance (2002) and Laureta (2008). The nomenclature was updated according to the WoRMS Editorial Board (2016). The biomass and species diversity (Shannon-Wiener diversity index,  $H'$ ) of the mollusc assemblages were determined per plot (three replicate plots per stand). The changes in species composition of mollusc assemblages with mangrove age and as affected by typhoon was assessed based on the distribution and the habitat and substrate preference of each mollusc species (using Plaziat, 1984; Matthes and Kapetsky, 1988; Lozouet and Plaziat, 2008; Printrakoon et al., 2008; and Palomares and Pauly, 2015).

#### 2.4. Data analyses

Variations in mollusc assemblages were analyzed using a non-parametric approach. Parametric tests were not possible because of heteroscedasticity of the data, even after data transformation. Sites

were categorized based on the stage of forest and sediment development (following Salmo et al., 2013), as: young (P6 and P8), intermediate (P10 and P11), mature (P12, P17, P18 and P50), and natural (Nx, Ny and Nz). A three-factorial Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001; Anderson et al., 2008) was used to test the differences in mollusc assemblages with developmental stage of the stands (factor 1), time (factor 2: pre-typhoon vs. 0.5-mo, 2.5-mo, 7-mo, and 9-mo post-typhoon), and typhoon (factor 3: impacted vs. un-impacted stands). The typhoon-impacted sites were P11 and P18 plantation stands. At 9-mo post-typhoon for factor 3, only the Ny and Nz (in Zambales) in natural stands were included in the analysis. No un-impacted sites from the mature stands were included in the analysis.

The raw data were permuted for a total number of 9999 permutations. A similarity matrix was constructed using the Bray-Curtis algorithm on standardized, log-transformed biomass data. Ordination was through non-metric multidimensional scaling (nMDS). To test the relationship between the mollusc assemblages and that of the vegetation and sediments, stepwise multiple regression analyses were applied on a correlation matrix (Sokal and Rohlf, 1997) separately between mollusc assemblages and vegetation and with sediment characteristics. From the resemblance matrix, the similarity percentage (SIMPER) procedure was used to determine the mollusc species that contributed to the similarities and dissimilarities between typhoon-impacted and unimpacted sites (Clarke and Warwick, 2001). The BEST-BIOENV procedure was used to compare the rank-similarity matrices for the mollusc assemblages with matrices created for the vegetation and sediment variables in 9999 permutations using datasets from Salmo et al. (2013, 2014). All multivariate analyses were conducted using PRIMER v6.1.12 (Clarke and Gorley, 2006).

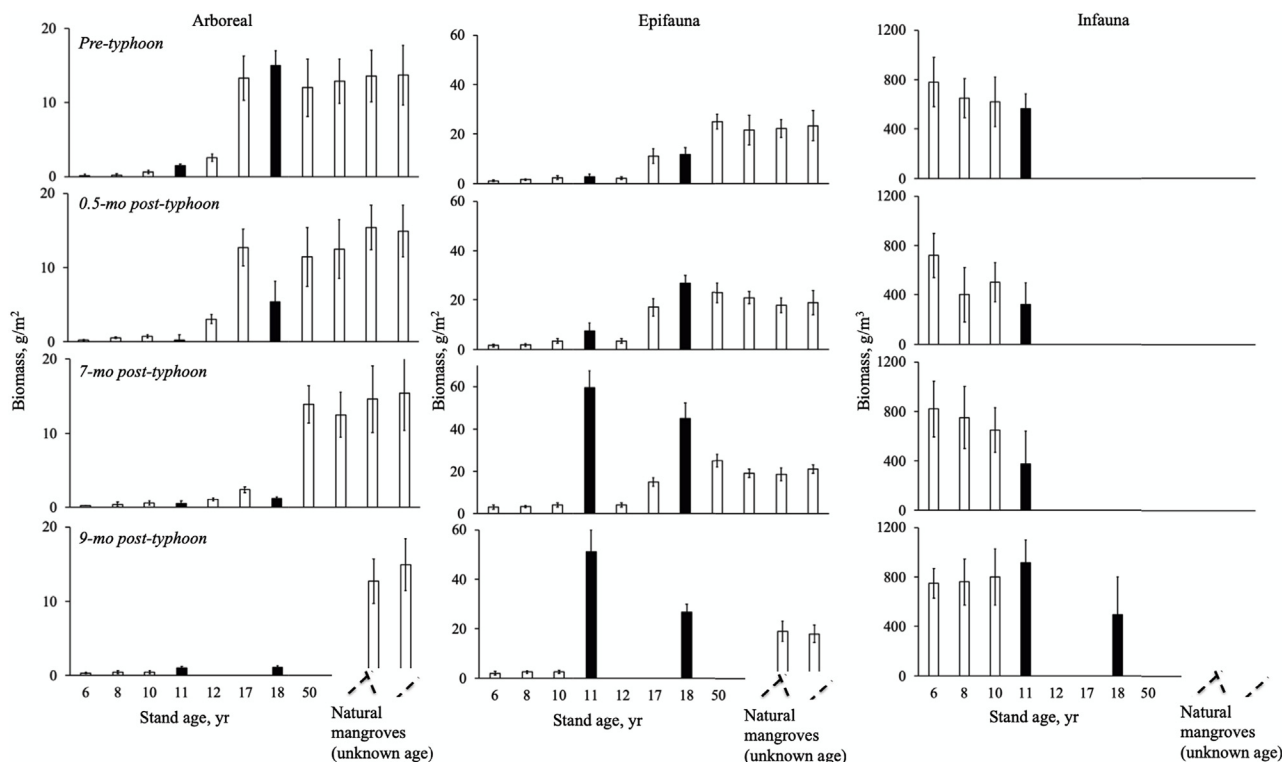


Fig. 2. Mean ( $\pm$  standard deviation) mollusc arboreal (left), epifaunal (middle) and infaunal (right) biomass showing contrasting changes after typhoon Chan-hom between typhoon-impacted (filled bars) and un-impacted (unfilled bars) sites.

### 3. Results

#### 3.1. Pre-vs post-typhoon changes in arboreal assemblage

A total of 10,625 individuals composed of 28 species from 16 families were recorded, of which the majority were gastropods (97 %; Supplemental Table 1). There were no significant differences in mollusc biomass among mangrove stands throughout the sampling periods, largely because of the high variability in each site. Prior to the typhoon, the pooled samples from each developmental stage yielded significant correlation between forest stage and biomass ( $Y = 88.603 \ln(x) - 122.67$ ;  $r^2 = 0.61$ ). Biomass was highest in the 18-yr old plantation (P18) with  $15 \pm 3 \text{ g m}^{-2}$  and was lowest in the 8-yr old plantation (P8) with  $0.30 \pm 0.01 \text{ g m}^{-2}$  (Fig. 2 left; see also Salmo et al., 2017). Species richness and diversity were lowest in the young mangrove stands, slightly higher in the intermediate stands, and peaked in the mature stands (Supplemental Fig. 1A). The patterns in biomass, species richness and diversity implied a clear progression of arboreal mollusc assemblage from young to intermediate, mature and natural stands (PERMANOVA test; Table 1A). These patterns were significantly correlated with the vegetation and sediment parameters. In the vegetation, the highest correlation coefficients were attributed to the combination of Leaf Area Index (LAI: 0.48) and above-ground biomass (AGB: 0.41;  $\rho = 0.51$ ;  $P < 0.001$ ; Table 2A), while for the sediment component, the combination of organic matter (% OM: 0.60), total nitrogen (TN: 0.47) and redox (0.44) had the highest correlation ( $\rho = 0.63$ ;  $P < 0.01$ ; Table 1A).

The occurrence of Typhoon Chan-hom resulted in 64–93 % reduction in arboreal mollusc biomass at the impacted sites (P11 and P18; Fig. 2, left). There was a continuous decline in arboreal mollusc biomass in P18 until 9-mo post-typhoon. In contrast, the arboreal mollusc biomass in P11 appeared to recover at 7- and 9-mo post-typhoon. The arboreal assemblages departed from their pre-typhoon stage groupings and this remained the case until 9-mo post-typhoon (Fig. 3, left). Both P11 and P18 transitioned to be closer to P6, P8 and P10 over time. The

mollusc assemblages varied significantly between the typhoon-impacted and un-impacted sites in all post-typhoon sampling periods ( $P < 0.01$ ; Table 1A). The SIMPER tests showed that the typhoon un-impacted and impacted sites had 82–86 % dissimilarity across post-typhoon periods (Table 3A). The species that contributed most to the dissimilarity were *T. sulcata*, *N. polita*, *P. cingulata* and *Cerithidea* sp. The typhoon-impacted sites had  $68 \pm 5$  % similarity and were characterized mainly by *T. sulcata*, *L. scabra* and *P. cingulata*. The species *T. sulcata* consistently characterized the impacted sites in all post-typhoon periods followed by *L. scabra* (until 2.5-mo post-typhoon, but replaced by *P. cingulata* at 7-mo and 9-mo post-typhoon). The un-impacted sites had  $69 \pm 4$  % similarity and were represented by *P. cingulata*, *N. polita*, *T. sulcata*, *L. scabra*, *N. planospira* and *Cerithidea* sp. The species *P. cingulata* and *L. scabra* consistently characterized the un-impacted sites in all post-typhoon periods. The species *T. sulcata*, *N. polita*, *N. planospira* and *Cerithidea* sp. had high scores at 0.5-mo, 2.5-mo, 7-mo and 9-mo post-typhoon period, respectively.

The post-typhoon changes in mollusc assemblage patterns were significantly associated with the changes in vegetation ( $\rho = 0.50$ ;  $P < 0.001$ ) and sediment parameters ( $\rho = 0.65$ ;  $P < 0.01$ ). Variables that had high correlation coefficients with mollusc biomass were the combinations of LAI (0.47) and AGB (0.40) in the vegetation, and OM (0.45), redox (0.45) and temperature (0.65) in the sediments (Table 2A). Significant correlations were more apparent between the mollusc assemblage and vegetation in all sampling periods than with sediment properties. In contrast, at 7-mo post-typhoon, the mollusc assemblage was not significantly associated with the sediment component, although significant correlation was again observed at 9-mo post-typhoon where % silt (0.53) and % OM (0.43) had high correlations (Table 2A).

#### 3.2. Pre-vs post-typhoon changes in epifaunal assemblage

Twenty-four species from 15 families were recorded out of the collected 5,986 epifaunal mollusc individuals (ca. 50 % lower than the

**Table 1**

Summary results of PERMANOVA test on changes in: (A) arboreal, (B) epifaunal, and (C) infaunal mollusc assemblages with mangrove developmental stages, time (pre-typhoon vs. post-typhoon) and typhoon effects (impacted vs. un-impacted sites). *P* denote significance at < 0.05 (\*), < 0.01 (\*\*); < 0.001 (\*\*\*); ns – not significant.

A. Arboreal				
Source	df	MS	Pseudo-F	P (permuted)
Stage	3	25,102	29.70	***
Time	3	5,686	6.73	***
Typhoon	1	7,974	9.43	***
Stage x Time	9	4,609	5.45	***
Stage x Typhoon	1	10,304	12.19	***
Time x Typhoon	3	3,228	3.82	***
Stage x Time x Typhoon	2	3,914	4.63	***
Residual	97	845		
Total	119			
B. Epifauna				
Source	df	MS	Pseudo-F	P (permuted)
Stage	3	36,994	54.81	***
Time	3	2,262	3.35	**
Typhoon	1	7,462	11.05	***
Stage x Time	9	1,837	2.72	***
Stage x Typhoon	1	5,863	8.69	***
Time x Typhoon	3	832	1.23	ns
Stage x Time x Typhoon	2	1,764	2.61	*
Residual	110	2,131		
Total	134			
C. Infauna				
Source	df	MS	Pseudo-F	P (permuted)
Stage	2	24,645	8.08	***
Time	4	7,626	4.61	***
Typhoon	1	8,029	4.02	***
Stage x Time	7	4,814	4.73	***
Stage x Typhoon	1	8,459	5.29	ns
Time x Typhoon	3	4,421	1.17	ns
Stage x Time x Typhoon	1	3,154	1.21	ns
Residual	73	1,655		
Total	92			

**Table 2**

Summary of BEST-BIOENV results showing association between (A) arboreal, (B) epifaunal, and (C) infaunal mollusc assemblages and vegetation and sediment characteristics for each sampling period. The variables that have high correlation coefficients are in bold fonts. Legend: LAI – Leaf Area Index, AGB – Above-Ground Biomass, OM – organic matter, TN – total nitrogen, AP – available phosphorus. *P* denote significance at < 0.01 (\*\*), < 0.001 (\*\*\*); ns = not significant.

Variables/Assemblages	A. Arboreal				B. Epifauna				C. Infauna			
	Time, pre- vs. post-typhoon				Time, pre- vs. post-typhoon				Time, pre- vs. post-typhoon			
	Pre-	0.5-mo	7-mo	9-mo post	Pre-	0.5-mo	7-mo	9-mo post	Pre-	0.5-mo	7-mo	9-mo post
<b>Vegetation</b>												
LAI	<b>0.48</b>	<b>0.47</b>	<b>0.47</b>	<b>0.47</b>	<b>0.47</b>	<b>0.43</b>	<b>0.48</b>	<b>0.57</b>	0.38	<b>0.47</b>	0.03	0.12
Tree density	0.26	0.26	0.39	0.30	0.24	0.21	0.36	0.23	<b>0.44</b>	-0.21	<b>0.56</b>	<b>0.41</b>
AGB	<b>0.41</b>	<b>0.40</b>	0.29	0.27	<b>0.42</b>	0.32	<b>0.42</b>	0.32	<b>0.47</b>	0.13	<b>0.44</b>	0.12
$\rho$	<b>0.51</b>	<b>0.50</b>	<b>0.57</b>	<b>0.48</b>	<b>0.48</b>	<b>0.44</b>	<b>0.56</b>	<b>0.58</b>	<b>0.50</b>	<b>0.47</b>	<b>0.56</b>	<b>0.44</b>
<i>P</i>	***	***	***	***	***	***	***	***	*	ns	***	**
<b>Sediment</b>												
Sand	0.07	0.07	0.01	0.39	0.27	0.31	0.05	<b>0.41</b>	<b>0.41</b>	-0.10	0.01	<b>0.41</b>
Silt	0.17	0.23	0.22	<b>0.53</b>	<b>0.41</b>	0.38	0.13	<b>0.43</b>	0.01	-0.28	0.10	0.31
OM	<b>0.60</b>	<b>0.45</b>	0.19	<b>0.43</b>	<b>0.59</b>	<b>0.45</b>	0.24	0.32	<b>0.48</b>	0.05	0.35	-0.02
TN	<b>0.47</b>	0.20	-0.07	0.31	0.23	0.22	0.04	0.20	0.11	-0.09	0.31	-0.06
AP	0.26	0.13	0.19	-0.02	0.17	-0.05	0.07	-0.03	-0.13	-0.16	<b>0.50</b>	0.01
Salinity	0.23	0.01	0.02	0.23	0.25	-0.01	-0.04	0.25	<b>0.45</b>	0.11	-0.18	0.01
pH	0.32	0.07	-0.18	0.09	0.16	-0.04	-0.14	0.17	-0.07	-0.06	-0.10	0.01
Redox	<b>0.44</b>	<b>0.45</b>	-0.22	0.08	0.38	0.35	-0.19	0.08	0.11	0.15	-0.14	-0.07
Temperature	0.20	<b>0.65</b>	-0.12	0.17	0.02	<b>0.43</b>	-0.17	0.11	-0.15	0.16	-0.05	-0.11
$\rho$	<b>0.60</b>	<b>0.65</b>	<b>0.33</b>	<b>0.53</b>	<b>0.60</b>	<b>0.58</b>	<b>0.28</b>	<b>0.50</b>	<b>0.51</b>	<b>0.26</b>	<b>0.55</b>	<b>0.42</b>
<i>P</i>	**	**	ns	***	**	***	ns	***	**	ns	**	**

collected arboreal assemblage), which comprised of 97 % gastropods and 3 % bivalves (Supplemental Table 1). Similar to the arboreal assemblage, there were no significant differences in epifaunal assemblages among stands, primarily because of the high variability among sites. The pooled samples per developmental stage showed significant negative correlation of epifaunal mollusc biomass with mangrove stage of development ( $Y = -15.48 \ln(x) + 73.82$ ;  $r^2 = 0.69$ ). The mean biomass for P11 and P18 was  $3 \pm 1 \text{ g m}^{-2}$  and  $12 \pm 3 \text{ g m}^{-2}$ , respectively. Species richness and diversity were high in young and intermediate plantations and lower in more mature and natural stands (Supplemental Fig. 1B). Prior to the occurrence of the typhoon, the epifaunal mollusc assemblages changed significantly with mangrove forest developmental stage (PERMANOVA test; Table 1B). The mollusc assemblages were significantly correlated with both the vegetation and sediment properties although the latter appeared to have stronger correlation. Highest correlation coefficients with epifaunal mollusc assemblages were attributed to the combinations of LAI (0.47) and AGB (0.42) for the vegetation ( $\rho = 0.48$ ;  $P < 0.001$ ) and % OM (0.59), and % silt (0.41) for the sediment properties ( $\rho = 0.60$ ;  $P < 0.01$ ; Table 2B; see Salmo et al., 2017).

Contrary to the arboreal assemblages, there was an increase in epifaunal assemblage's biomass in impacted sites by 62–95 % for P11 and 56–64 % for P18 from pre-typhoon to 7-mo post-typhoon. Both impacted sites then had reduced biomass at 9-mo post-typhoon (Fig. 2, middle). There was a significant difference between the typhoon-impacted and un-impacted stands in all post-typhoon sampling periods ( $P < 0.01$ ; Table 1B). The mollusc assemblage in P11 became more similar to the younger plantations (P6 & P8) after the typhoon while P18 completely separated from all groups (Fig. 3, middle). The typhoon un-impacted and impacted sites had 72–78 % dissimilarity. The dissimilarity increased from 0.5-mo to 7-mo post-typhoon but slightly decreased at 9-mo post-typhoon (Table 3B). The species that contributed most to the dissimilarity between the un-impacted and impacted sites were *T. sulcata* and *P. cingulata*. The typhoon-impacted sites had  $82 \pm 5$  % similarity and were characterized by *T. sulcata* and *P. cingulata*. The similarity decreased from 89 % (at 0.5-mo post-typhoon) to 69 % (at 7-mo post-typhoon) but increased to 92 % at 9-mo post-typhoon. The un-impacted sites had  $83 \pm 4$  % similarity and were characterized by *P. cingulata*, *L. scabra*, *L. philberti* and *N. polita*,

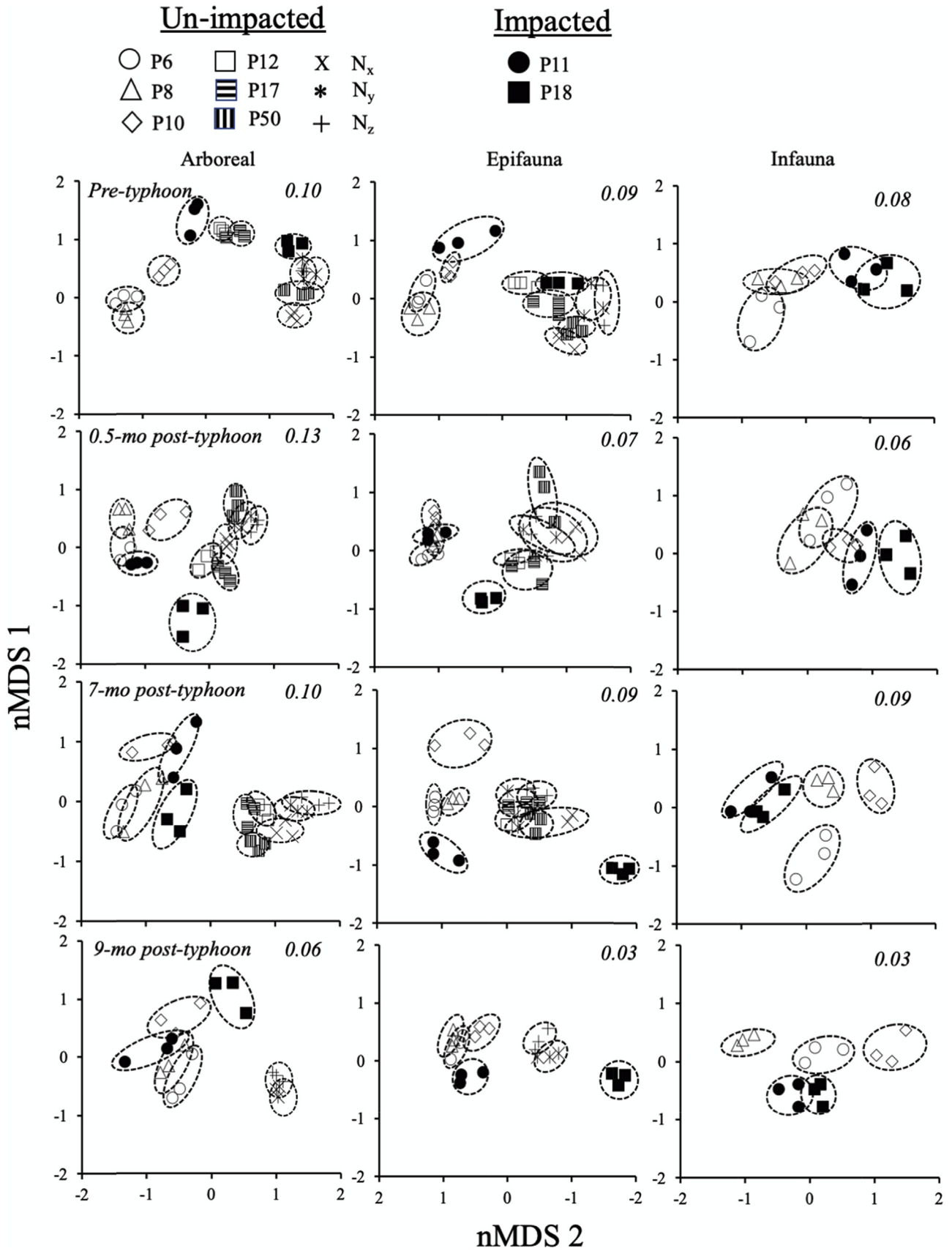


Fig. 3. Non-metric multi-dimensional scaling (nMDS) plots of arboreal (left), epifauna (middle) and infauna (right) mollusc assemblages showing shifts from pre-typhoon (cf. Salmo et al., 2017) to post-typhoon (at 0.5-mo post-typhoon; 7-mo post-typhoon; and 9-mo post-typhoon). Ellipse denote grouping for each mangrove forest age. The numbers on the top right of each plot denote the stress level.

**Table 3**

Summary results of SIMPER analysis showing the arboreal, epifaunal and infaunal mollusc species that contributed most strongly to dissimilarity (top) and similarity (bottom) between typhoon-unimpacted and impacted sites. Species are listed in order of their percent contribution to similarities and dissimilarities.

Assemblage	Post-typhoon period							
	0.5-mo		2.5-mo		7-mo		9-mo	
A. Arboreal	86.05		82.69		85.22		85.04	
	<i>T. sulcata</i>		<i>T. sulcata</i>		<i>T. sulcata</i>		<i>T. sulcata</i>	
	<i>N. polita</i>		<i>P. cingulata</i>		<i>P. cingulata</i>		<i>P. cingulata</i>	
	<i>P. cingulata</i>				<i>N. polita</i>		<i>Cerithidea</i> sp.	
	Unimpacted, 74.72	Impacted, 57.15	Unimpacted, 59.86	Impacted, 63.77	Unimpacted, 62.98	Impacted, 78.39	Unimpacted, 77.64	Impacted, 73.42
<i>P. cingulata</i>	<i>T. sulcata</i>	<i>P. cingulata</i>	<i>T. sulcata</i>	<i>P. cingulata</i>	<i>T. sulcata</i>	<i>P. cingulata</i>	<i>T. sulcata</i>	
<i>N. polita</i>	<i>L. scabra</i>		<i>L. scabra</i>	<i>L. scabra</i>	<i>L. scabra</i>	<i>P. cingulata</i>	<i>P. cingulata</i>	
<i>T. sulcata</i>		<i>N. polita</i>		<i>N. planospira</i>		<i>Cerithidea</i> sp.	<i>P. cingulata</i>	
B. Epifauna	75.96		76.14		78.48		72.45	
	<i>T. sulcata</i>		<i>P. cingulata</i>		<i>T. sulcata</i>		<i>C. cingulata</i>	
	<i>P. cingulata</i>		<i>T. sulcata</i>		<i>P. cingulata</i>		<i>T. sulcata</i>	
	76.08	88.89	86.43	77.78	77.50	68.89	93.97	91.60
	<i>P. cingulata</i>	<i>T. sulcata</i>	<i>P. cingulata</i>	<i>T. sulcata</i>	<i>P. cingulata</i>	<i>T. sulcata</i>	<i>P. cingulata</i>	<i>T. sulcata</i>
	<i>T. sulcata</i>	<i>P. cingulata</i>	<i>L. philberti</i>	<i>P. cingulata</i>	<i>T. sulcata</i>	<i>P. cingulata</i>	<i>N. polita</i>	<i>P. cingulata</i>
	<i>L. philberti</i>				<i>N. polita</i>		<i>T. sulcata</i>	
C. Infauna	80.83		65.32		79.51		71.52	
	<i>T. nodifera</i>		<i>A. perspectiva</i>		<i>P. cingulata</i>		<i>P. cingulata</i>	
	<i>P. cingulata</i>		<i>P. cingulata</i>		<i>C. urceus</i>		<i>A. nodifera</i>	
	<i>A. cornea</i>				<i>A. nodifera</i>		<i>N. polita</i>	
	44.69	28.23	51.57	43.66	40.38	21.09	45.76	27.76
	<i>P. cingulata</i>	<i>A. nodifera</i>	<i>P. cingulata</i>	<i>P. cingulata</i>	<i>P. cingulata</i>	<i>P. cingulata</i>	<i>P. cingulata</i>	<i>P. cingulata</i>
	<i>N. polita</i>	<i>P. cingulata</i>	<i>L. philberti</i>	<i>N. polita</i>	<i>N. polita</i>	<i>C. urceus</i>	<i>N. polita</i>	<i>A. nodifera</i>
	<i>C. urceus</i>							

although *T. sulcata* also had high score at 7-mo and 9-mo post-typhoon. The similarity among un-impacted sites fluctuates with sampling periods.

The changes in mollusc assemblages were significantly correlated with both vegetation ( $\rho = 0.44$ ;  $P < 0.001$ ) and sediment characteristics but not with sediment at 7-mo post-typhoon ( $\rho = 0.58$ ;  $P < 0.001$ ; Table 3). For vegetation, LAI consistently appeared to have high correlation with the mollusc assemblage followed by AGB. For sediments, the reduction in % OM (0.45) and increased temperature (0.43) had the highest correlation at 0.5-mo post-typhoon but this was changed at 9-mo post-typhoon when % sand (0.41) and % silt (0.43) had higher correlations.

### 3.3. Pre-vs post-typhoon changes in infaunal assemblage

A total of 1,406 individuals composed of 12 species from 10 families were collected from young, intermediate and mature mangrove plantations in Lingayen Gulf, but not in other more mature plantations and natural mangroves (Supplemental Table 1). Species richness, diversity, and biomass were highest in the youngest plantation and decreased with age of the stands. There was a significant negative correlation of infaunal biomass ( $62.78 \pm 25.11 \text{ g m}^{-3}$ ;  $Y = -436.3 \ln(x) + 1248.1$ ;  $r^2 = 0.72$ ) with stand age. Infaunal mollusc assemblages significantly varied with age of the forest stands showing a clear pattern from young to intermediate plantations through to mature plantations (PERMANOVA test; Table 1C). The infaunal mollusc assemblages were significantly correlated with vegetation and sediment characteristics. The combinations of AGB (0.47) and tree density (0.44) for the vegetation characteristics ( $\rho = 0.50$ ;  $P < 0.05$ ; Table 3a), and % OM (0.48), salinity (0.45), and % sand (0.41) for the sediment characteristics ( $\rho = 0.51$ ;  $P < 0.01$ ; Table 2C) had the highest correlation coefficients.

There was a 40–60 % reduction in infaunal mollusc biomass between pre-typhoon and 0.5-mo post-typhoon. However, there was a 50–70 % increase in infaunal mollusc biomass from 0.5-mo to 9-mo post-typhoon (Fig. 2, right). There was a significant difference between pre-typhoon and post-typhoon infaunal mollusc assemblages that

persisted until 9-mo post-typhoon (PERMANOVA test; Table 1C; Fig. 3, right). The infaunal assemblage varied between typhoon-impacted and un-impacted sites ( $P < 0.05$ ). The typhoon-impacted sites differed significantly with developmental stage and with time. There were, however, no significant interactions between time and typhoon, and among mangrove developmental stages (Table 1C). The typhoon un-impacted and impacted sites had 65–81 % dissimilarity and tended to decrease with time (Table 3C). The species that distinguished the typhoon un-impacted from impacted sites differed with the arboreal and epifaunal assemblages, and with periods. In the impacted sites, the species *P. cingulata* consistently appeared across all post-typhoon periods but other species that had high scores were *T. nodifera* and *C. urceus* at 0.5-mo post-typhoon, *A. perspectiva* at 2.5-mo post-typhoon, *C. urceus* and *A. nodifera* at 7-mo post-typhoon and *A. nodifera* and *N. polita* at 9-mo post-typhoon. The un-impacted sites had higher similarity at 40–46% (with high contribution from *P. cingulata*, *N. polita*, *C. urceus*, and *L. philberti*) than the typhoon-impacted sites (21–44 %; with high contribution from *A. nodifera* and *P. cingulata*). In the impacted sites, *N. polita* and *C. urceus* had high scores at 7-mo and 9-mo post-typhoon.

The post-typhoon changes in the infaunal assemblages were associated with variations in both the vegetation and sediment characteristics although the variables that showed significant correlation varied over time. The infaunal assemblage was significantly correlated with vegetation and sediment parameters at 7-mo and 9-mo post-typhoon, but not at 0.5-mo post-typhoon. The combination of tree density (0.56) and AGB (0.44) had the highest correlation with the changes at 7-mo ( $\rho = 0.56$ ;  $P < 0.001$ ) and 9-mo post-typhoon ( $\rho = 0.44$ ;  $P < 0.01$ ). The mollusc assemblage was significantly correlated with sediment characteristics at 7-mo ( $\rho = 0.55$ ;  $P < 0.01$ ) and 9-mo post-typhoon ( $\rho = 0.42$ ;  $P < 0.01$ ) but not at 0.5-mo post-typhoon. The combination of Available Phosphorus (AP) content (0.50) and % sand (0.41) had the highest correlation with the infaunal assemblage.



#### 4. Discussion

A total of 38 species from 23 families were collected from all sites which is comparable to the mature and natural *Rhizophora* mangroves in SE Asia (see Salmo et al., 2017) – 26 in natural stands in Selangor, Malaysia (Sasekumar, 1974), 34 in natural and planted mangroves in Ranong, Thailand (Macintosh et al., 2002), and 44 in nearly pristine mangroves in Sarawak, Malaysia (Ashton et al., 2003). Consistent with published reports, only a few taxa (at most 5–9) dominate at each site (Sasekumar, 1974; Tolhurst and Chapman, 2007). Prior to the typhoon, a clear separation between the groups of young and intermediate stands as compared to the groups of mature and natural stands was manifested (Salmo et al., 2017). Moreover, the mollusc assemblages between mature plantations and natural stands did not vary. In all assemblage types, similarity among planted and natural stands always began at the 11<sup>th</sup> year of the mangrove stands. A similar mollusc colonization pattern (with mangrove age) was also reported in mangroves from New Zealand (Morrisey et al., 2003).

The combination of changes to vegetation and sediment characteristics resulted in post-typhoon changes in mollusc assemblages (Table 3). It is not straightforward, however, to identify a single particular variable that causes the changes since vegetation and sediments are interrelated, although at some point certain variables show higher correlation. For example, in arboreal mollusc assemblage, the reductions in LAI and AGB had significant correlation at 0.5-mo post-typhoon, but as time progressed, it appeared that forest cover alone had a more direct effect than either tree density or AGB. At 7-mo and 9-mo post-typhoon, both tree density and AGB were in continuous decline while LAI regenerated, although very slowly. The increase in LAI coincided with the re-establishment of other mollusc species which possibly indicates recovery. For sediment parameters, the reductions in OM coupled with low redox values and elevated temperatures were associated with the arboreal mollusc assemblage at 0.5-mo post-typhoon. At 9-mo post-typhoon, when redox and temperature appeared to be near pre-typhoon values, only OM and silt had a significant association with the arboreal and epifaunal mollusc assemblages. For infaunal mollusc assemblages, association with sediment changes were manifested at 7-mo post-typhoon, which was attributed almost solely to increased AP content. This possibly implies a lag period since AP enhancement occurred at 0.5-mo post-typhoon (Salmo et al., 2014). The post-typhoon changes in vegetation and sediment conditions in typhoon-impacted sites, and with time, were reported in Salmo et al. (2014).

##### 4.1. Altered mollusc colonization and trajectory patterns

Typhoon Chan-hom caused significant changes in arboreal, epifaunal, and infaunal mollusc assemblages in typhoon-impacted sites. There are very few studies on the effects of typhoons on the dynamics of mangrove-dependent fauna (Smith et al., 1994) thus comparisons of the present study with published data are wanting. To our knowledge, this study reports the first account on changes in mollusc assemblages affected by a catastrophic typhoon. Perhaps the closest comparison that could be made is the loss of forest cover brought about by deforestation in Gazi Bay, Kenya (Fondo and Martens, 1998; Bosire et al., 2008) and habitat modification in Moreton Bay, Australia (Skilleter and Warren, 2000). These studies pointed out that any level of disturbance may affect the diversity and biomass of molluscs. The loss of forest cover and impoverished sediment conditions (anoxic and warm sediments) translates into loss or reduction of food and shelter for molluscs.

Changes in the biomass of molluscs manifested immediately after the typhoon but varied with assemblage type (Figs. 2 and 3; Table 1). For arboreal mollusc assemblage, there was an immediate reduction in P18 and did not appear to recover even at 9-mo post-typhoon. In P11 however, there was an immediate biomass reduction only at 0.5-mo post-typhoon but appeared to recover at 9-mo post-typhoon (Fig. 2, left). Such differences may imply more intense damage in P18 than in

P11 as there were more trees that died in the older stands. The P18 have taller trees and are thus more prone to wind impacts.

The reduction in food and habitat may have forced arboreal molluscs to move from the vegetation and instead colonized the sediment surface. Hence, there was a sudden increase in epifaunal biomass (but notably with higher contribution from *T. sulcata*; Table 3) up to 7-mo post-typhoon although it declined at 9-mo post-typhoon. Prior to the occurrence of the typhoon, the epifaunal assemblage in the P11 stands were dominated by *P. cingulata* and *T. nodifera*. Then, in all post-typhoon periods, the contribution of *T. sulcata* increased up to 60%. At 7-mo post-typhoon, the re-vegetation observed in P11 (but not in P18) may have provided canopy shades and reduced the effect of higher sediment temperatures. The infaunal assemblage had a different fate, where an immediate reduction in P11 occurred at 0.5-mo post-typhoon but recovered thereafter. In P18, infaunal molluscs emerged only at 9-mo post-typhoon. The changes in infaunal assemblage coincided with the degraded vegetation and sediment conditions (because of reduced canopy cover and increased temperature, respectively), particularly with the dumping of fine sediments after the typhoon. From these patterns, it can also be inferred that the sediment column may have been in a more favorable condition to attract molluscs than the vegetation similar to what was observed in the epifaunal assemblages.

Species composition in all assemblages in the impacted sites changed dramatically after the typhoon. Our findings contrast those of Diele et al. (2013) who studied the impacts of typhoons in sesarmid crabs in 18 to 20-yr old mangrove plantations in Vietnam. They reported no significant departure from pre-typhoon crab assemblages, and posited that crabs are robust against typhoons. Molluscs however, may have higher dependence to mangrove vegetation and sediments than crabs. Dominant species that were recorded prior to the typhoon were either severely reduced or completely lost, but this was more apparent in arboreal assemblages. The sustained dominance of *P. cingulata* and *T. sulcata* in P11 and P18 throughout the sampling periods, respectively, may indicate the adaptedness (or possible greater resilience) of these species to disturbance. Re-emergence of other pre-typhoon species occurred two months earlier in infaunal and epifaunal assemblages as compared to the arboreal molluscs. We also observed the sudden increased in dominance (by at least 60%) of the species *Littoraria scabra* (in P11) and *Telescopium telescopium* (in P18) starting at 7-mo post-typhoon. Such emergence as a co-dominant species may be a response to the altered environment. These species are known to be an indicator of the stage of mangrove development in intermediate and mature stage stands (see Salmo et al., 2017). Thus, such sudden dominance may also indicate that the restoration trajectory could have been turned back by 10–15 years, which is the age of the intermediate and mature stands. Post-typhoon mollusc recolonization pattern probably suggest that mollusc recovery will occur first with the infaunal and epifaunal assemblages until such time as the vegetation and sediment condition takes to re-establish, to allow the recruitment of arboreal molluscs.

##### 4.2. Implications and prospects of post-typhoon recovery

Post-typhoon recovery of mangrove forest cover may be improved in plantation stands with appropriate site selection and substrate-species matching. Comparable with other forest types, mangrove plantations have increased structure (as tree density and biomass) with stand age (Salmo et al., 2013). In this way, as vegetation maturity progresses, there is simultaneous progress in the colonization and build-up of mollusc assemblages (Salmo et al., 2017) as well as in nekton communities (Salmo et al., 2018). These and other fauna are attracted to mangroves because of the food and habitat provided by the developing forest stands. Furthermore, most of the mollusc and nekton species found in mangroves are economically important for coastal residents as sources of food and livelihood resources (Tabuchi, 2004; Peralta-Milan and Salmo, 2013). It is important to appreciate that this provisioning of

food and livelihoods derived from mature mangrove plantations encourages coastal residents to participate in mangrove planting programs (Salmo et al., 2007).

Most mangrove plantations in the Philippines are monospecific (using the *Rhizophora* genus) and inappropriately designed. These plantations are often located in sub-optimal planting sites (see Primavera and Esteban, 2008, for example). Hence, mangrove plantations often have stunted growth and poor survival (Samson and Rollon, 2008). Even if stands reach > 20 yrs and look similar to natural stands (Salmo and Juanico, 2015), most mangrove plantations have low structural complexity. These stands display delayed development by at least 10 years (Salmo et al., 2013), as compared to natural mangrove forest growth under natural canopy gap regeneration (cf. Duke, 2001). When hit by a catastrophic typhoon, severe damage to vegetation structure, such as high tree mortalities (resulting in reduced tree density and biomass) leads to impoverished sediment conditions (like high temperature and salinity). While such damage is similarly manifested in adjacent natural mangrove stands, the species that are mainly from the genera *Avicennia* and *Sonneratia* have coppiced and show refoliation (SS & NCD pers. obs.). Such resprouting and recovery capability is evident in *Avicennia*-dominated stands damaged during an extreme weather event (Duke et al., 2017). In contrast, *Rhizophora* species do not recover asexually (see Duke, 2001). These differences in growth and response capabilities amongst different mangrove species is rarely considered in assessments of severe disturbance. The altered habitat recovery trajectories in turn equate to losses in food and habitat leading to reductions in mollusc assemblages, and more importantly affecting their restoration trajectories (Fig. 3; Table 2).

In November 2017 (ca. 8-yr post-typhoon), the damaged plantation showed few signs of recovery, although the 11-yr stands (P11, now 19-yr old) had some refoliation and those P18 trees that survived (now 26-yr old) remained defoliated. Seedling densities in both damaged stands were either very low or undetectable. In contrast, natural stands nearing P18 had completely refoliated, although the canopy cover was still at < 60 % and some trees showed signs of decay. High seedling densities and some saplings were observed in the forest floor (mainly *Avicennia* sp. and *Sonneratia* sp.). We observed some molluscs (primarily *T. telescopium*, *L. scabra* and *N. polita*) either attached to the seedlings or on the sediment surface. Molluscs are known bioturbators in which their burrowing and feeding activities could provide aeration to mangroves (Zvonareva et al., 2015). It is possible that the post-typhoon seedling and sapling recruits provide spaces for mollusc to colonize. In return, these mollusc assemblages may have similarly assisted the mangroves to grow and possibly to recover. Such observations were lacking in the damaged mangrove plantations. Given the beneficial role that molluscs likely contribute to mangrove recovery, we suggest an assessment of mollusc assemblages be included as an indicator in studies of post-typhoon recovery.

Prospects for mollusc recovery are unclear. Complete recovery will depend on the rate of recovery and re-establishment of both vegetation and sediment conditions to pre-typhoon levels. If ever they recover, the critical variables would be the re-establishment of forest cover and the enhancement of organic matter in the sediment. The regeneration pathway may follow the pre-typhoon pattern, starting with the infaunal and epifaunal assemblages first and when the forest recovers the colonization of arboreal faunal assemblage may commence.

## 5. Conclusions

A catastrophic typhoon resulted in the alteration of the restoration trajectory of mollusc assemblages. But the damage was more evident in more mature stands than in intermediately old stands. Post-typhoon changes in mollusc assemblages were attributed to the sudden reduction or loss of their sources of habitat and food. Shifts in dominant mollusc species from pre-typhoon to post-typhoon in all assemblages were attributed to changes in vegetation and sediment conditions.

Moreover, the severe reduction in the vegetation (mainly through tree density and canopy cover) caused the molluscs to occupy the sediment. As molluscs are known bioturbators, the sudden changes in mollusc assemblages may have also contributed to the delayed recovery of the mangrove forest.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2019.106365>.

## References

- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral. Ecol* 26, 32–46.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK, pp. 214.
- Ashton, E.C., Macintosh, D.J., Hogarth, P.J., 2003. A baseline study of the diversity and community ecology of crab and molluscan macrofauna in the Semantan mangrove forest, Sarawak, Malaysia. *J. Trop. Ecol.* 19, 127–142.
- Bosire, J.O., Dahdouh Guebas, F., Walton, M., Crona, B.L., Lewis III, R.R., Field, C., Kairo, J.G., Koedam, N., 2008. Functionality of restored mangroves: a review. *Aquat. Bot.* 89, 251–259.
- Busby, P.E., Motzkin, G., Boose, E.R., 2008. Landscape-level variation in forest response to hurricane disturbance across a storm track. *Can. J. For. Res.* 38 (12), 2942–2950.
- Cairns, J., Heckman, J.R., 1996. Restoration ecology: the state of an emerging field. *Ann Rev Energy Environ* 21, 167–189.
- Cannicci, S., Burrows, D., Fratini, S., Smith III, T.J., Offenberg, J., Dahdouh-Guebas, F., 2008. Faunal impact on vegetation structure and ecosystem function in mangrove forests: a review. *Aquat. Bot.* 89, 186–200.
- Chapman, M.G., Tolhurst, T.J., 2007. Relationships between benthic macrofauna and biogeochemical properties of sediments at different spatial scales and among different habitats in mangrove forests. *J. Exp. Mar. Biol. Ecol.* 343, 96–109.
- Cinco, T.A., de Guzman, R.G., Ortiz, A.M.D., Delfino, R.J.P., Lasco, R.D., Hilario, F.D., Juanillo, E.L., Barba, R., Ares, E.D., 2016. Observed trends and impacts of tropical cyclones in the Philippines. *Int. J. Climatol.* 36 (14), 4638–4650.
- Clarke, K.R., Gorley, R.N., 2006. PRIMER V6: User Manual/tutorial. PRIMER-E, Plymouth
- Craighead, Jr., F.C., Gilbert, V.C., 1962. The effects of Hurricane Donna on the vegetation of southern Florida. *Fla. Sci.* 25, 1–28.
- Clarke, K.R., Warwick, R., 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd. PRIMER-E, Plymouth.
- Dance, S.P., 2002. Shells (Smithsonian Handbooks). DK Publishing. pp. 256 New York.
- Diele, K., Tran Ngoc, D.M., Geist, S.J., Meyer, F.W., Pham, Q.H., Saint-Paul, U., Tran, T., Berger, U., 2013. Impact of typhoon disturbance on the diversity of key ecosystem engineers in a monoculture mangrove forest plantation, Can Gio Biosphere Reserve, Vietnam. *Glob. Planet. Chang.* 110, 236–248.
- Duke, N.C., Kovacs, J.M., Griffiths, A.D., Preece, L., Hill, D.J.E., Oosterzee, P.V., Mackenzie, J., Morning, H.S., Burrows, D., 2017. Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: a severe ecosystem response, coincidental with an unusually extreme weather event. *Mar. Freshw. Res.* 68 (10), 1816–1829. <https://doi.org/10.1071/MF16322>.
- Duke, N.C., 2001. Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems. *Wet. Ecol. Manag.* 9, 257–269.
- Everham III, E.M., Brokaw, N.V.L., 1996. Forest damage and recovery from catastrophic wind. *Bot. Rev.* 62 (2), 113–185.
- Fondo, E.N., Martens, E.E., 1998. Effects of mangrove deforestation on macrofaunal densities, Gazi Bay, Kenya. *Mangroves Salt Marshes* 2, 75–83.
- Gardiner, B.A., Quine, C.P., 2000. Management of forests to reduce the risk of abiotic damage – a review with particular reference to the effects of strong winds. *For. Ecol. Manag.* 135, 261–277.
- Kathiresan, K., Bingham, B.L., 2001. Biology of mangroves and mangrove ecosystems. *Adv. Mar. Biol.* 40, 81–251.
- Kitamoto, A., 2009. Typhoon 200902 (Chan-hom). [internet] [Updated 22 Feb 2013; cited 22 Feb 2013]. Available from: <http://agora.ex.nii.ac.jp/digital-typhoon/summary/wnp/1/200902.html.en>.
- Kubota, H., Chan, C.L., 2009. Interdecadal variability of tropical cyclone landfall in the

- Philippines from 1902 to 2005. *Geophys. Res. Lett.* 36, L12802.
- Lantican, R.M., 2001. The Science and Practice of Crop Production. Southeast Asian Ministers of Education Organization (SEAMEO), SEAMEO Regional Center for Graduate Study and Research in Agriculture (SEARCA), and University of the Philippines Los Baños (UPLB), Laguna, Philippines.
- Laureta, L.V., 2008. Compendium of the Economically Important Seashells in Panay. University of the Philippines Press, Quezon City, pp. 147.
- Lozouet, P., Plaziat, J.-C., 2008. Mangrove Environments and Molluscs: Abatan River, Bohol and Panglao Islands, Central Philippines. Conchbooks, Hackenheim, Germany, pp. 160.
- Macintosh, D.J., Ashton, E.C., Havanon, S., 2002. Mangrove rehabilitation and intertidal biodiversity: a study in the Ranong mangrove ecosystem, Thailand. *Estuar. Coast Shelf Sci.* 55, 331–345.
- Matthes, H., Kapetsky, J.M., 1988. Worldwide Compendium of Mangrove-Associated Aquatic Species of Economic Importance 814. FAO, Rome FAO Fishery Circular No. 328.
- Morrissey, D.J., Skilleter, G.A., Ellis, J.I., Burns, B.R., Kemp, C.E., Burta, K., 2003. Differences in benthic fauna and sediment among mangrove (*Avicennia marina* var. *australasica*) stands of different ages in New Zealand. *Estuar. Coast Shelf Sci.* 56, 581–592.
- Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.-O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: a review. *Aquat. Bot.* 89, 155–185.
- Netto, S.A., Galucci, F., 2003. Meiofauna and macrofauna communities in a mangrove from the islands of Santa Catalina, South Brazil. *Hydrobiologia* 505, 159–170.
- Palomares, M.L.D., Pauly, D., 2015. SeaLifeBase, world wide web electronic publication. version 10/2015. [www.sealifebase.org](http://www.sealifebase.org).
- Peralta-Milan, S.A., Salmo III, S.G., 2013. Evaluating patterns of fish assemblage changes from different-aged reforested mangroves in Lingayen Gulf. *J. Environ. Sci. Manag.* 16 (1), 11–19.
- Plaziat, J.C., 1984. Mollusc distribution in the mangal. In: Por, F.D., Dor, I. (Eds.), *Hydrobiology of the Mangal*. W. Junk, the Hague, pp. 111–143.
- Printrakoon, C., Wells, F.E., Chitramvong, Y., 2008. Distribution of molluscs in mangroves at six sites in the Upper Gulf of Thailand. *Raffles Bull. Zool.* 8 (S), 247–257.
- Primavera, J.H., Esteban, J.M.A., 2008. A review of mangrove rehabilitation in the Philippines: successes, failures and future prospects. *Wetlands. Ecol. Manag.* 16 (5), 345–358.
- Ruiz-Jaen, M.C., Aide, T.M., 2005. Restoration success: how is it being measured? *Restor. Ecol.* 13 (3), 569–577.
- Salmo III, S.G., Juanico, D.E., 2015. An individual-based model of long-term forest growth and carbon sequestration in planted mangroves under salinity and inundation stresses. *Int. J. Philipp. Sci. Technol.* 8, 31–35.
- Salmo III, S.G., Tibbetts, I., Duke, N.C., 2017. Colonization and shift of mollusc assemblages as a restoration indicator in planted mangroves in the Philippines. *Biodivers. Conserv.* 26, 865–881.
- Salmo III, S.G., Tibbetts, I., Duke, N.C., 2018. Nekton communities as indicators of habitat functionality in Philippine mangrove plantations. *Mar. Freshw. Res.* 69 (3), 477–485.
- Salmo III, S.G., Torio, D.D., Esteban, J.M.A., 2007. Evaluation of rehabilitation strategies and management schemes for the improvement of mangrove management programs in Lingayen Gulf. *Sci. Diliman* 19 (1), 24–34.
- Salmo III, S.G., Lovelock, C.E., Duke, N.C., 2013. Vegetation and soil characteristics as indicators of restoration trajectories in restored mangroves. *Hydrobiologia* 720, 1–18.
- Salmo III, S.G., Lovelock, C.E., Duke, N.C., 2014. Assessment of vegetation and soil conditions in restored mangroves interrupted by severe tropical typhoon ‘Chan-hom’ in the Philippines. *Hydrobiologia* 733, 85–102.
- Samson, M.S., Rollon, R.N., 2008. Growth performance of planted mangroves in the Philippines: revisiting forest management strategies. *Ambio* 37 (4), 234–240.
- Sasekumar, A., Chong, V.C., 1998. Faunal diversity in Malaysian mangroves. *Glob. Ecol. Biogeogr. Lett.* 7, 57–60.
- Sasekumar, A., 1974. Distribution of macrofauna on a Malayan mangrove shore. *J. Anim. Ecol.* 43, 51–69.
- Skilleter, G.A., Warren, S., 2000. Effects of habitat modification in mangroves on the structure of molluscs and crab assemblages. *J. Exp. Mar. Biol. Ecol.* 244, 107–129.
- Smith III, T.J., Robblee, M.B., Wanless, H.R., Doyle, T.W., 1994. Mangroves, hurricanes, and lightning strikes. *Bioscience* 44, 252–262.
- Sokal, R.R., Rohlf, F.J., 1997. *Biometry: the Principles and Practice of Statistics in Biological Research*, third ed. WH Freeman and Company, New York.
- Tabuchi, R., 2004. The rehabilitation of mangroves in Southeast Asia. In: Saxena, K.G., Liang, L., Kono, Y., Miyata, S. (Eds.), ‘Small-Scale Livelihoods and Natural Resources Management in Marginal Areas: Case Studies in Monsoon Asia. Proceedings of an International Symposium’, 29–30 October 2003, Tokyo, Japan. United Nations University, Tokyo, Japan 121–128.
- Tolhurst, T.J., Chapman, M.G., 2007. Patterns in biogeochemical properties of sediments and benthic animals among different habitats in mangrove forests. *Austral. Ecol.* 32, 775–788.
- WoRMS Editorial Board, 2016. World register of marine species. <http://www.marinespecies.org>, Accessed date: 9 December 2017 Accessed.
- WXTide32, 2016. WXTide32. <http://www.wxtide32.com/>.
- Zvonareva, S., Kantor, Y., Li, X., Britayev, T., 2015. Long-term monitoring of Gastropoda (Mollusca) fauna in planted mangroves in central Vietnam. *Zool. Stud.* 54, 39. <https://doi.org/10.1186/s40555-015-0120-0>.