

Research paper

Deciphering the synergistic impact of elevated temperature and oil pollution on meiobenthic community structure: A benthocosm study

Moumita Ghosh, Sumit Mandal*

Marine Ecology Laboratory, Department of Life Sciences, Presidency University, 86/1, College Street, Kolkata 700073, India



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ABSTRACT

Meiobenthos has been considered as an excellent tool for biomonitoring assessment. Elevated temperature and oil pollution are considered as the most pervasive aspects of global environmental changes and matter of concern for contemporary society. Presently, very limited information is available about the synergistic effect of these stressors on meiobenthic community structure and tolerance potential from tropical intertidal environment. Here, we assessed their impacts on meiobenthic community by conducting a 60 days long benthocosm experiment selecting three sets of temperature (25°, 30° and 35 °C) and two sets of diesel oil (low and high) combinations. Gradual changes in their community composition were revealed discernibly with exposures to both the disturbances after 30 and 60 days of experimental period. Diversity profiles for the nematodes were less affected, but copepods showed a graded response of decreasing density with increasing dose of both the stressors. Other meiobenthic taxa such as halacarid mite, turbellaria and polychaete juveniles were adversely affected and eliminated from the treatments, howbeit abundance of ostracods, foraminiferans and bivalve settlers varied significantly. A 3-factor PERMANOVA indicated a significant effect of temperature, diesel, between their interaction and interaction among stressors and time on meiofaunal abundances. In case of free-living nematodes, temperature rise and diesel contamination synchronously led to an elimination of *k*-selected species like *Halalaimus gracilis*, *H. longicaudatus*, *Oxystomina aersetosa* and *Pomponema* sp. with a significant decrease in abundance of *H. capitulatus* and *Oncholaimus* sp. The *r*-selected species *Daptonema invagiferum*, *Sabatieria praedatrix*, *Theristus acer*, *Monhystera* sp. and *Thalassomonhystera* sp. had endured even at high doses of diesel treatment in three different temperatures set up. The effects were evident in term of changes in life strategies with an increment of opportunistic species and increased trophic diversity of deposit feeders in treated sediments. Overall, elevated temperature together with diesel oil contamination were found to alter species dynamics within shallow intertidal meiobenthic communities, which might have significant Armageddon on benthic ecosystem functioning.

1. Introduction

Several anthropogenic disturbances wrecked havoc on marine ecosystems, thereby altering the essential services they provide (Harley et al., 2006; Rosenzweig et al., 2008). Climate change induced elevated temperature has already jeopardized marine ecosystem functioning (Richardson and Schoeman, 2004; Behrenfeld et al., 2006; Poloczanska et al., 2016). Since the post-industrial era, excessive combustion of fossil fuel unambiguously leads to a noticeable increase in ocean mean temperature and it is conjectured that by 2100 sea surface temperature (SST) would escalate up to 2–4 °C (Collins et al., 2013; IPCC, 2014). A warming trend in the SST along the coastal Bay of Bengal has been

observed during last few decades (Samanta et al., 2018) and has potential reverberation on coastal marine biota. Sea surface warming substantially declines primary production in tropical region (Krumhardt et al., 2017), which may affect the availability of food (organic matter) for benthic organisms. As benthic compartments play vital roles in biogeochemical cycles (Nascimento et al., 2012) and energy transfer to commercially important benthivorous fishes, shrimps and crabs (Schückel et al., 2013; Schratzberger and Ingels, 2017), impact to benthic community structure may have cascading ecological effects in marine food chains. In addition, distributional shift of benthic invertebrates as well as impact on their reproductive success and offspring survivability have been reported in response to warming waters

* Corresponding author.

E-mail address: sumit.dbs@presiuniv.ac.in (S. Mandal).<https://doi.org/10.1016/j.ecoenv.2020.111549>

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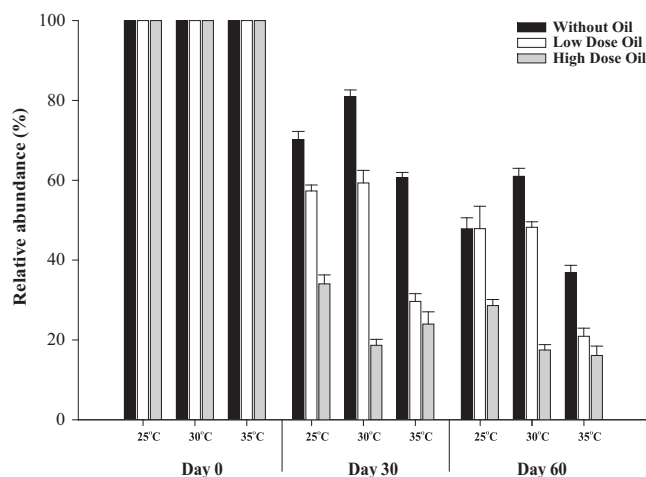


Fig. 1. Relative abundance % of meiobenthos (mean ± SD) (after square-root transformation) observed during benthocosm experiment, exposed to different treatments.

(Holbrook et al., 2020 and references therein). Compared to Open Ocean, shallow coastal marine habitats, especially intertidal organisms, are more susceptible to elevated sea surface as well as air temperature due to diel exposure during low tides (Alsterberg et al., 2011; Harley et al., 2006). Apart from elevated temperature, diurnal temperature range, both in frequency and magnitude, is also expected to increase in the forthcoming years and impose severe pressure on a wide array of living organisms (Easterling et al., 2000; Pachauri et al., 2014). Such temperature extremes may severely affect the fitness and/or interaction of intertidal species, as these species are already impoverished due to several other stressors (e.g. habitat destruction, chemical pollution) (Vafeiadou et al., 2018a). Furthermore, additional impact may lead to extinction of the most vulnerable species which could have further

ramification on ecosystem functioning (Danovaro et al., 2004a; Lejeune et al., 2010). Generally, species belong to tropical region are characterized as stenotherms and have narrow thermal tolerance window than their temperate counterparts (Deutsch et al., 2008). Therefore, the predicted temperature rise in upcoming decades may further exacerbate the alteration of tropical community dynamics putting ecological services at risk.

It is now unequivocally accepted that marine ecosystems are under the threat of petroleum hydrocarbon pollution and its adverse effects on marine biota are global environmental concern since petroleum hydrocarbons are toxic to all forms of life (Arnberg et al., 2018; Honda and Suzuki, 2020). Due to their hydrophobicity and persistent nature, hydrocarbons tend to adsorb quickly onto suspended particulate materials

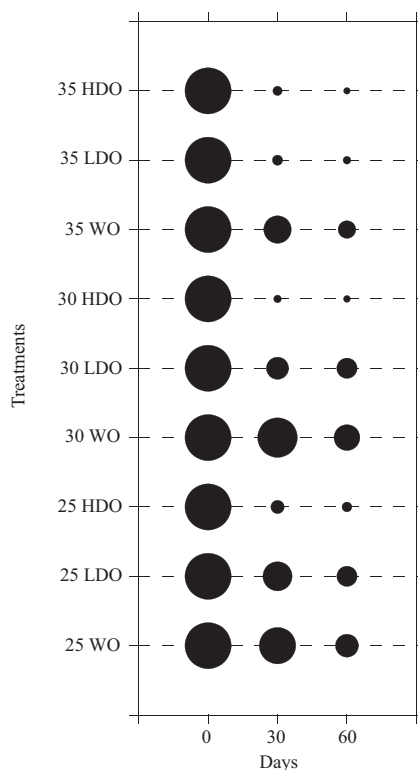


Fig. 2. Treatment-wise variation in the relative abundance % of nematode community during three different time periods. Data were scaled using the square-root function. The maximum symbol diameter corresponds to 100%.

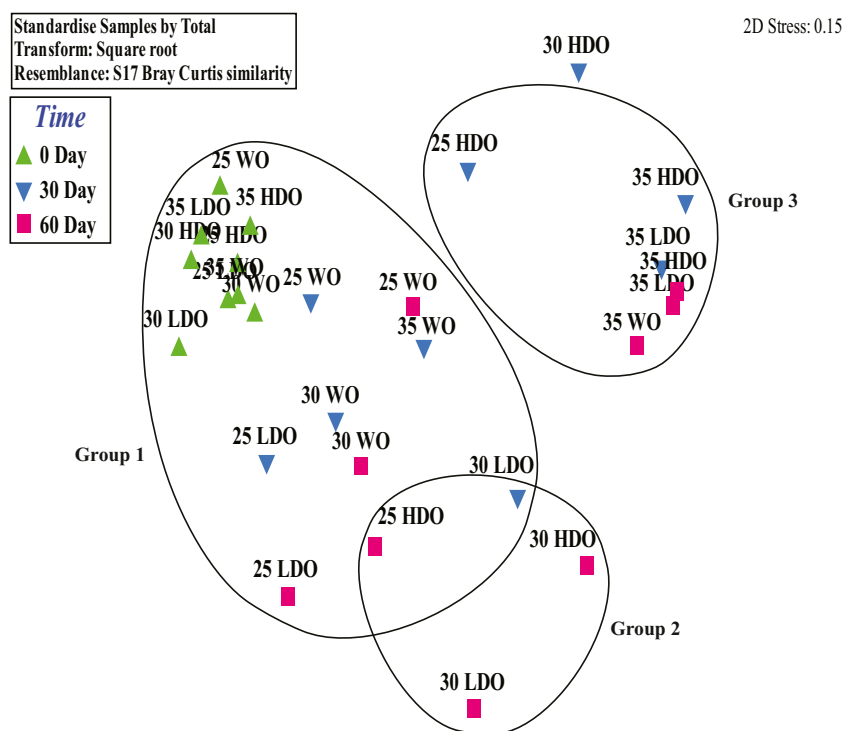


Fig. 3. nMDS ordination plot of nematode species composition using Bray–Curtis similarity matrix from two different treatments (temperature and diesel pollution). 25: 25 °C, 30: 30 °C, 35: 35 °C; WO: without oil, LDO: low dose of oil, HDO: high dose of oil.

along with sediment and exert direct impact on benthic animals via bioaccumulation (Boonyatumanond et al., 2006; Perugini et al., 2007), attenuating their physiological performances. Contaminants are likely to be transmitted to higher trophic levels via food chain and moreover, bioaccumulation could inflict severe risks for human health as a result of fishery products consumption. Blessed with unique geographic position, India significantly relies on marine environment for maritime trades and capture fisheries. In last couple of decades to support the increasing demands of market, coastal fishing activities have burgeoned remarkably in India (CMFRI, 2017) leads to an increased risk of oil spills from mechanized fishing vessels and ships. Most of the oil spills are generally taken place from fishing vessels, tourist boats, shipwrecks, oil refinery explosions, oil well blowout, vessel collision, leaking pipeline and operational discharges.

Meiobenthos are size-based benthic invertebrates and contribute significantly in the physical, chemical and biological properties of marine sediments (Coull, 1999; Giere, 2009). Additionally, meiobenthic organisms can be used as proxy to environmental changes due to their small sizes, ubiquitous distribution, higher abundance, fast generation cycles and direct benthic development (Vanaverbeke et al., 2011; Zepilli et al., 2015). Anthropogenic perturbation induced any alteration to their community structure might have a profound repercussion on the entire food web dynamics. Free-living nematodes, the most abundant meiofaunal taxon, encompass an exceptionally high structural and functional diversity (Heip et al., 1985; Giere, 2009). Their short life cycles, limited vagility and semi-permeable cuticles (direct contact with sediment particles) make them suitable yardstick to study anthropogenic disturbances. Therefore, shifts in nematode community structure could be an excellent bio-indicator of environmental stress in marine ecosystems (Schratzberger and Warwick, 1999; Schratzberger et al., 2007).

Owing to their significance in the marine food chain, a considerable research have been conducted to understand possible detrimental effects of elevated temperature on meiofaunal community structure (Danovaro et al., 2004a; Gingold et al., 2013; Meadows et al., 2015; Lee et al., 2017; Mevenkamp et al., 2018; Vafeiadou et al., 2018a, 2018b). Globally,

effects of petroleum hydrocarbon on metazoan meiofauna and nematodes have equally been covered separately in existing literature through mesocosm studies (Mahmoudi et al., 2005; Beyrem et al., 2007; Elarbaoui et al., 2015; Kang et al., 2016). Despite extensive research efforts, there remains a dearth of baseline data on stress responses of ocean warming in combination with oil pollution on meiobenthic communities, particularly on nematode species composition from tropical ecosystem. Majority of the prior works have been concentrated on individual species response by providing single stressor. Therefore, considering different species have different tolerance range, multiple global stressors impact study on community level might be a new approach for tropical benthic entities. Moreover, global climate anomaly coupled with other anthropogenic pressures is supposed to reduce the resilience of marine inhabitants as mirrored by potential detrimental cascading impact. Thus, it is imperative to understand the effects of both the disturbances on shallow water meiobenthic biodiversity. We hypothesized that combined impact of elevated temperature and oil pollution would cause more adverse effects on meiobenthic community structure than temperature or oil alone.

2. Materials and methods

2.1. Sample collecting site

Natural meiobenthic sediments were collected from an unpolluted intertidal site (21°38'44.49"N; 87°37'26.49"E) of coastal Bay of Bengal, eastern side of India. On the sampling day, the ambient pore water temperature, salinity, dissolved oxygen (DO) and pH were recorded as 25 °C, 25.5 PSU, 4.12 mg L⁻¹ and 7.9 respectively. Sediments of the study area was mainly composed of sand (85.35%) and 0.32% of organic carbon.

2.2. Sample collection

Sediments were collected from monthly lowest low tidal range of a sandflat during low tide followed by chart datum. We randomly

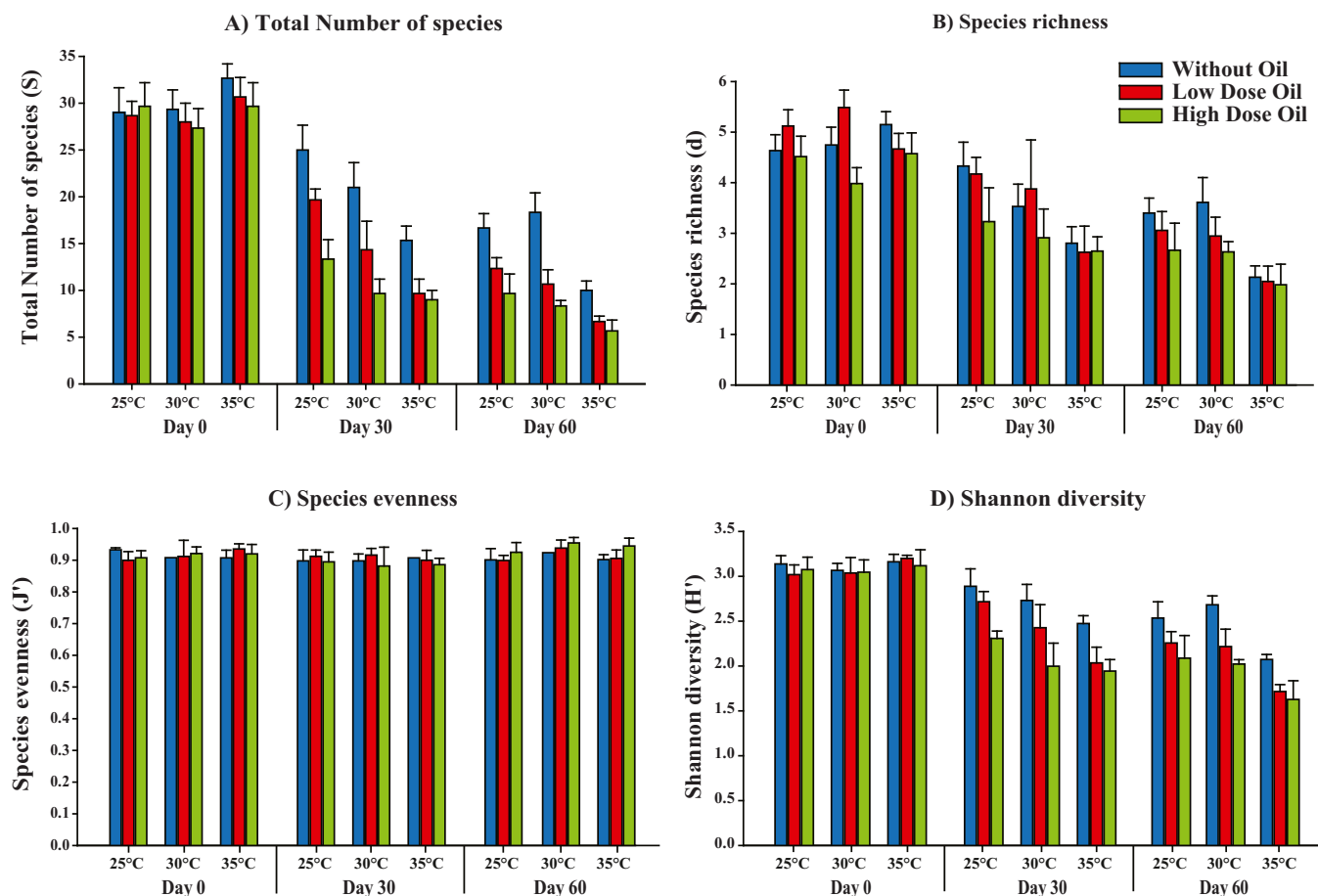


Fig. 4. Graphical summary of univariate indices for nematode assemblages from each benthocosm.

collected upper 2 cm of the sediments in a large tank with a shovel and carefully homogenized them by gentle mixing with a large spatula. We restricted sediment collection up to top 2 cm as more than 90% meiofauna are observed in upper 2–3 cm (Schratzberger et al., 2004; Allouche et al., 2020). Homogenized sediments then carefully washed in situ through a 500 μm sieve using filtered sea water (20 μm) to remove macrofauna, shell debris and pebbles (Wigley and McIntyre, 1964). Sieved sediments were then placed in food grade plastic aquaria (40 \times 28 \times 20 cm), up to 5 cm sediment depth to avoid anoxic condition. A total of nine plastic aquaria with sieved sediments were returned to the laboratory. Field collected filtered sea water (20 μm) was carefully added to each aquarium up to 5 cm above the sediment surface and left for 48 h for acclimatization (Schratzberger et al., 2004) prior to the experiments. Light was controlled in a 12/12 h light/dark cycle and seawater aeration of each aquarium was ensured with continuous moderate oxygen bubbling without causing any disturbance to the sediment.

Ambient pore water temperature, salinity, dissolved oxygen (DO) and pH were recorded at the time of sampling by using handheld thermometer, salinity refractometer (Master-S/Mill Alpha, Atago), DO (Orion Star A223 dissolved oxygen/RDO portable meter kit) and pH meter (Orion star A211) respectively. Sediment organic carbon and sediment texture (sand, silt and clay %) were analyzed following El Wakeel and Riley (1957) sieve and pipette method (Folk, 1968) correspondingly.

2.3. Experimental design

Three large water baths (80 \times 50 \times 40 cm) were used for the experiments and in each water bath three sediment filled plastic aquaria

were half-submerged. One aquarium was used for temperature treatment and remaining two were treated with low and high concentration of diesel oil respectively (Supplementary Fig. S1). Temperature of each water bath was maintained by submerged digital thermostat for the entire duration of the experiment (60 days) (Schratzberger et al., 2004). Three temperature treatments were used: a) control temperature (25 $^{\circ}\text{C}$), corresponded to the ambient pore water temperature at sampling time and b) two elevated temperatures: 30 $^{\circ}\text{C}$: as experienced by Bay of Bengal during summer (Chanda et al., 2018; Saikranthi et al., 2019) and 35 $^{\circ}\text{C}$: as predicted by IPCC (2014). A transparent plastic cover with perforation was used in each aquarium to prevent evaporation and subsequent salinity changes. During the experiment, salinity was checked daily and adjusted as and when required using distilled water.

Two separate doses (low and high) of lead-free diesel were applied to the corresponding treatments of two plastic aquaria and remaining one aquarium was without diesel dose in each water bath. Sediment in each plastic aquarium was contaminated by appropriate doses of diesel to obtain low (5 mg kg^{-1}) and high concentration (20 mg kg^{-1}). Doses of diesel were selected by the description of Mahmoudi et al. (2005). Diesel was introduced into the sediment with the help of a sprayer. Contaminated sediments of each aquarium were topped up with filtered sea water (20 μm) collected during sampling and were aerated using aquarium air stone.

A total of nine treatments were used and the benthocosm experiment continued for 60 days (Supplementary Fig. S1). Treatments included: 25 $^{\circ}\text{C}$ without oil (25 $^{\circ}\text{C}$ WO) as control, 25 $^{\circ}\text{C}$ with low dose of oil (25 $^{\circ}\text{C}$ LDO), 25 $^{\circ}\text{C}$ with high dose of oil (25 $^{\circ}\text{C}$ HDO), 30 $^{\circ}\text{C}$ without oil (30 $^{\circ}\text{C}$ WO), 30 $^{\circ}\text{C}$ with low dose of oil (30 $^{\circ}\text{C}$ LDO), 30 $^{\circ}\text{C}$ with high dose of oil (30 $^{\circ}\text{C}$ HDO), 35 $^{\circ}\text{C}$ without oil (35 $^{\circ}\text{C}$ WO), 35 $^{\circ}\text{C}$ with low dose of oil (35 $^{\circ}\text{C}$ LDO) and 35 $^{\circ}\text{C}$ with high dose of oil (35 $^{\circ}\text{C}$ HDO).

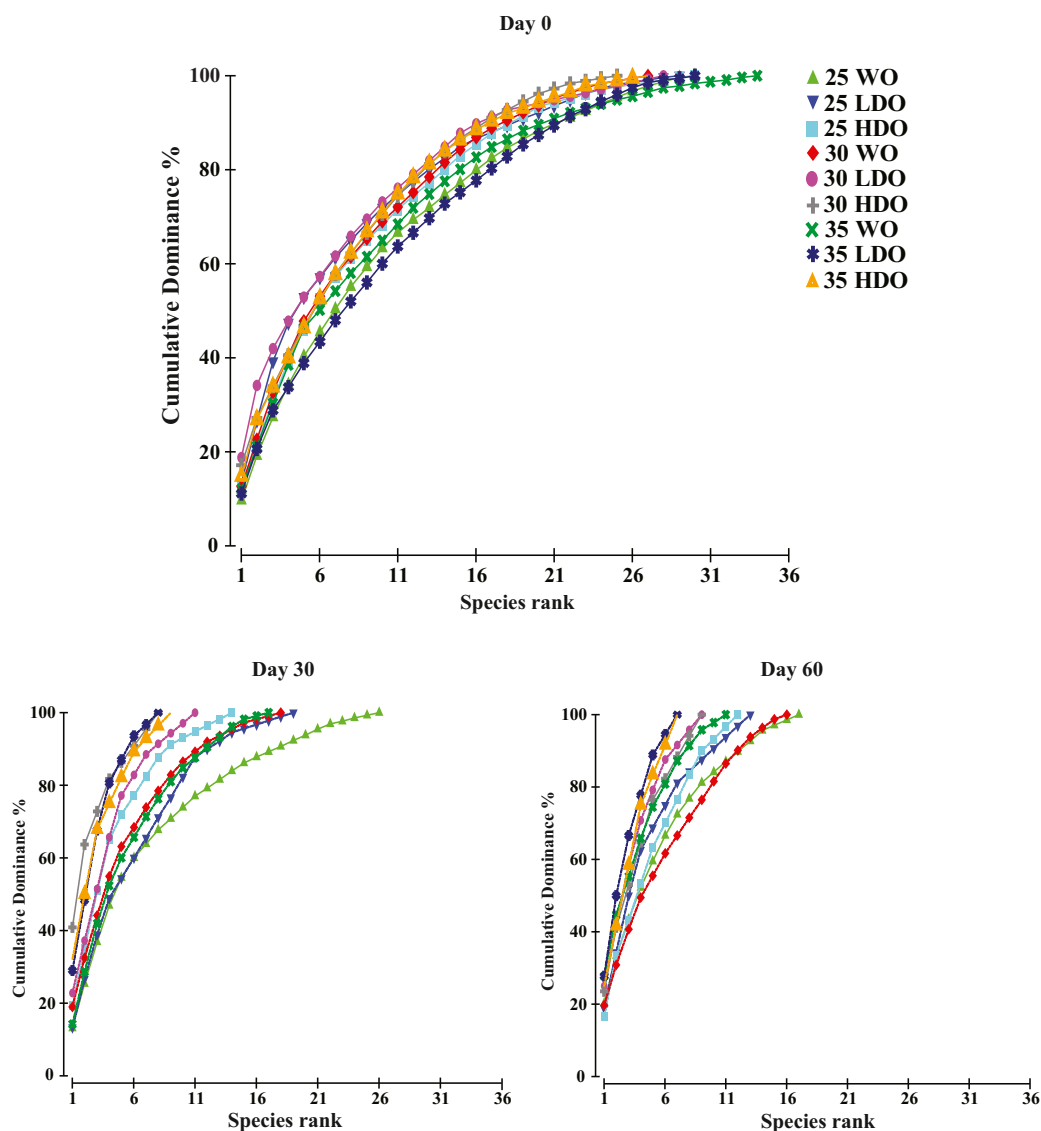


Fig. 5. The k -dominance curves of nematode composition among different treatments for uncontaminated (day 0) and post treatment communities (day 30 and 60). 25: 25 °C, 30: 30 °C, 35: 35 °C; WO: without oil, LDO: low dose of oil, HDO: high dose of oil.

2.4. Faunal analyses

Triplicate samples were collected prior to onset of the experiment (day 0), after 30 and 60 days from the respective experimental setup. A 50 ml syringe (inner diameter 3 cm) was used to collect the sediment and preserved in 4% buffered Rose Bengal (0.5 g L^{-1}) formalin (Dano-[varo et al., 2004b](#)) for further analysis. Meiofaunal organisms were sorted, enumerated and identified up to major taxonomic level. Furthermore, from each experimental setup, individual nematode species was mounted on glass slide with the help of anhydrous glycerin (Vincx, 1996) for identification up to species level under a compound microscope fitted with a camera (Nikon ECLIPSE Ci) following standard pictorial keys (Platt and Warwick, 1983, 1988; Warwick et al., 1998) and the literature present in the database: NeMys (Bezerra et al., 2020).

2.5. Data analyses

Non-metric multidimensional scaling (nMDS) was performed based on average relative abundance of nematodes measured in each replicate using Bray-Curtis similarity matrix (square-root transformed data). Similarity profile (SIMPROF) test was carried out to detect significantly

important station groups (significance level 0.05). Similarity of percentages (SIMPER) analysis was used to identify the key species responsible for the formation of groups. The following ecological indices were determined depending upon nematode abundances: Shannon-Wiener (H'), Margalef's species richness (d) and Pielou's evenness (J'). Permutational Multivariate Analysis of Variance (PERMANOVA) was applied to examine the effects of elevated temperature, diesel and their interaction on experimental meiobenthos, nematode and all the ecological indices. The design included three factors: temperature (fixed factor with three levels; 25 °C, 30 °C and 35 °C), dose of diesel (fixed factor with three levels; WO, LDO and HDO) and time (fixed factor with three levels; 0, 30 and 60 day). When significant effects ($p < 0.05$) of the selected factors were observed, pairwise tests were also carried out, to identify each factor separately in each level from other factor.

The k -dominance curves of the cumulative abundance percentage among free-living nematode species rank were also constructed to assess dominance patterns and species diversity in different treatments. In this curve, the percentage abundance of each nematode species is plotted cumulatively in a decreasing order of dominance against the species rank (Lambshhead et al., 1983). All statistical analyses were conducted using PRIMER (version 6) software (Clarke and Gorley, 2006; Clarke

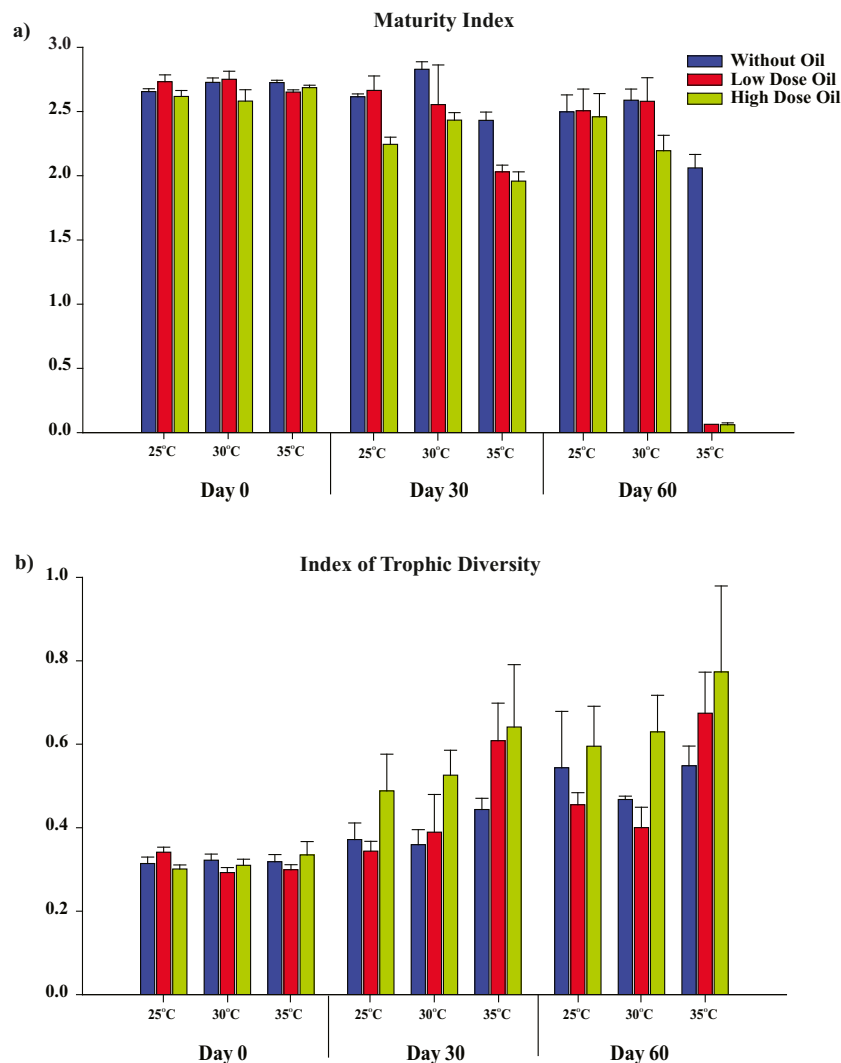


Fig. 6. Nematode a) Maturity Index and b) Index of Trophic Diversity in each treatment group.

et al., 2008) equipped with add-on package PERMANOVA (Anderson et al., 2008). Based on nematode community structure, two different functional diversity measures, namely Maturity Index (MI) (Bongers, 1990) and Index of Trophic Diversity (ITD) (Heip et al., 1985; Ferris and Bongers, 2009) were also analyzed to procure a comprehensive set of community descriptors. MI was calculated as $MI = \sum v(i) \times f(i)$, where $v(i)$ is the c-p value of the taxon i and $f(i)$ is the frequency of the taxon i . Colonizer–persister or c-p value is assigned to each nematode genus based on their colonization ability; ranging from 1 (rapid colonizer and highly tolerable to stress: r -strategists) to 5 (poor colonizer and highly susceptible to stress: persisters or k -strategists) (Bongers, 1990). ITD was calculated as $ITD = \sum \theta_i^2$, where θ_i is the abundance of the i^{th} trophic guild. According to Wieser's (1953) classification, nematodes were assigned to four trophic guilds: selective deposit feeders or essentially bacterivores (1A), non-selective deposit feeders or opportunistic feeders (ingest microalgae, bacteria etc.) (1B), epistrate feeders or herbivores (2A) and predators or omnivores (2B). Microsoft Excel was used to calculate these indices. Prior to analyses, meiobenthos and nematode abundances data were normalized by applying square-root transformation. Variations in meiobenthic relative abundances, MI, ITD and all the ecological indices were plotted in SigmaPlot (version 11.0; developed by Systat Software, San Jose, CA). The differences in the nematode community structure in all treatments were illustrated by bubble plot using SURFER 8 program (developed by Golden Software Inc., USA).

3. Results

3.1. Meiofauna abundances

The graphical summary of average meiofaunal relative abundance percentages from each benthocosm depicted clear effects of the two specific disturbances after 30 and 60 days of experimental period (Fig. 1). Among meiobenthic taxa, free-living nematodes dominated the community structure throughout the experiment followed by harpacticoid copepod and also displayed extreme compositional shift in terms of abundance against treatments. Other meiofauna taxa like, halacarid mite, turbellaria and polychaete juveniles were adversely affected and eliminated from the treatments, howbeit abundance of ostracods, foraminiferans and bivalve settlers varied significantly. A 3-factor PERMANOVA ($p < 0.05$) indicated a significant effect of temperature ($p = 0.001$), diesel ($p = 0.001$), between their interaction ($p = 0.001$) and interaction among stressors and time ($p = 0.001$) on meiofaunal abundances (Supplementary Table S1). Pairwise test revealed significant differences ($p < 0.05$) between temperature and dose of diesel oil (except 30 °C and 35 °C at HDO).

3.2. Species composition of nematode assemblages

There was a notable decrease in the percentage of relative abundance of nematode communities in stressors induced benthocosm treatments

compared to control (Fig. 2). PERMANOVA ($p < 0.05$) also revealed significant variations at the scale of temperature, diesel and their interaction (Supplementary Table S1). Pairwise tests showed significant effects ($p < 0.05$) between temperature and dose of diesel oil (except 30 °C and 35 °C at HDO). A total of thirty six nematode species were identified during the experimental period. Prior to onset of the experiment, all benthocosms were characterized by a significant high numbers of *Daptonema invagiferoum*, *Marylynnia complexa*, *Sabatieria praedatrix*, *Theristus acer* and *Viscosia abyssorum*. However, their abundance declined sharply in diesel amended sediments rather than elevated temperature treatments alone. Increasing level of stressors, both temperature and diesel contamination led to an elimination of *k*-selected species like *Halalaimus gracilis*, *H. longicaudatus*, *Oxystomina aetosa* and *Pomponema* sp. with a significant decrease in the abundance of *H. capitulatus* and *Oncholaimus* sp. The *r*-selected species *Monhystera* sp., *Thalassomonhystera* sp., *D. invagiferoum*, *S. praedatrix* and *T. acer* had endured even at high doses of diesel from three different temperature (25, 30 and 35 °C) set up (25 °C HDO, 30 °C HDO and 35 °C HDO).

Nematode species dependent multivariate nMDS ordination plot showed three different groups (group 1, 2 and 3) and a separate treatment (30 °C HDO – 30 day) (Fig. 3). SIMPER analysis identified nematode species *D. invagiferoum* and *M. complexa* to be mainly responsible for the formation of group 1 and 2. On the other hand, along with *D. invagiferoum*; *S. praedatrix*, *T. acer* and *V. abyssorum* were main contributors for the formation of group 3 (Supplementary Table S2). Graphical representation of univariate indices for nematode community from each benthocosm depicted a clear effect of treatments over time. Total number of nematode species (*S*), species richness (*d*), evenness (*J'*) and Shannon – Wiener index (*H'*) decreased considerably with the increasing level of disturbances (Fig. 4). PERMANOVA tests showed that total number of nematode species ($p < 0.05$), species richness ($p < 0.05$) and Shannon–Wiener index ($p < 0.05$) were significantly affected by single factor temperature, diesel dose and time, but not by their interaction (Supplementary Table S1). Nematode species evenness was neither affected by single factor temperature nor diesel dose. The *k*-dominance curves based on the nematode abundance data of each species reflected a distinct comparative dominance pattern in respect to time in each treatment (Fig. 5). From day 0 to day 60, the elevation of each curve illustrated a clear trend of decreasing diversity with increasing level of stressors. On day 30 post treatment, the highest diversity (lowermost curve) was found at control benthocosm (25 °C WO), whereas lowest diversity (uppermost curve) was observed at 30 °C HDO. Furthermore, after 60 days, the curves revealed that treatments with diesel contaminated sediment of 35 °C set up (35 °C LDO and 35 °C HDO) were characterized by the lowest taxonomic diversity.

Prior to application of the two selected disturbances, nematode species exhibited all kind of colonizer-persister classes (c-p 1–4), except c-p 5, where c-p 2 and 3 codominant followed by c-p 4 and 1. Higher MI values (2.58 ± 0.09 – 2.75 ± 0.06) at pre-treatment communities indicated a stable environment, whereas after 30 and 60 days, MI decreased with the increasing level of the two selected disturbances. However, the lowest MI was recorded as 0.06 ± 0.01 on 60 days treated benthocosm (35 °C HDO) (Fig. 6a). Enrichment opportunist (c-p 1) species *Monhystera* sp. and *Thalassomonhystera* sp. and general opportunists (c-p 2) like *D. invagiferoum*, *S. praedatrix* and *T. acer* were found in this community. A stable ITD was observed at control benthocosm treatment; albeit treated communities reflected a declining trend of diversity corresponds to increased ITD (Fig. 6b). PERMANOVA tests revealed that the maturity index was significantly affected by temperature ($p = 0.001$), diesel dose ($p = 0.001$), time ($p = 0.001$) and their interaction ($p = 0.001$). On contrary, the index of trophic diversity was significantly affected by temperature ($p = 0.001$), diesel dose ($p = 0.001$) and time ($p = 0.001$) separately, however the interaction of the disturbances did not evoke a significant effect (Supplementary Table S1).

4. Discussion

Understanding the potential impacts of anthropogenic induced changes on the meiobenthic communities and its consequences on ecosystem functioning is a priority to better forecast the probable outcome in future. In recent years, unprecedented increase of greenhouse gas emissions from industries and other anthropogenic activities are making the world warmer, disrupting rainfall patterns, increasing the frequency of extreme weather events and driving marine ecosystems at the high risk of fundamental ecological transformation. Long-term effects of elevated temperature are posing a serious threat to ocean productivity and food web dynamics, by shifting species distributions, impacting fisheries and crippling economic activity (Behrenfeld et al., 2006; Halpern et al., 2008). Here we explored the community level responses of meiofauna and nematodes against a 5 °C increment of temperature (25 vs. 30 vs. 35 °C) and increased diesel oil concentration (5 vs. 20 mg kg⁻¹) in synergy, which gave insight into the trade-off between the experimental organisms and underlying causes that regulated their community changes. In the present study, a dramatic impoverishment of meiofaunal abundance was detected after 30 and 60 days of experimental trail in treated benthocosm. Individual meiofaunal taxa responded differentially to varying degree of treatments. More specifically, nematode, copepods and foraminiferal densities were negatively affected by elevated temperature and diesel oil concentrations with the exception of ostracods that seemed to be positively correlated. This result is in agreement with Vafeiadou et al. (2018b) for nematode communities from a tropical intertidal location under elevated constant temperature. Gingold et al. (2013) also reported negative effect of high temperature on two subtropical nematode assemblages, which is in accordance with the present observations. Similar to our study, Mevenkamp et al. (2018) described declining trends of harpacticoid copepods to warming water. On contrary, abundance of ostracod remained relatively unaffected by both the disturbances. This finding is fully comparable with the results acquired from a mesocosm experiment that documented significant increases of ostracods with regard to increases of lead concentrations (Frontalini et al., 2018). Ostracods are generally recognized as very sensitive fauna to anthropogenic perturbations; however, their adaptive behaviors to environmental stress have also been documented elsewhere (Zeppilli et al., 2015 and references therein).

Meiofauna are also known to be influenced by hydrocarbon pollution and their communities, in general, declined in response to acute toxicity (Schratzberger et al., 2003; Veiga et al., 2010; Montagna et al., 2013; Kang et al., 2014, 2016). A sharp decline in copepod abundance compared to nematodes in oil contaminated benthocosm clearly indicated a community level trophic response. Different hydrocarbon pollutants trigger indigenous benthic bacterial production, which might act as food resources for opportunistic bacterivore nematode species (Montagna et al., 2013). Therefore, lack of food presumably caused copepod communities to be outcompeted from other meiofaunal counterparts. However, a contrasting trend was observed in case of ostracod and bivalve settlers as their densities remained slightly affected during the experimental period in hydrocarbon treatments. This phenomenon might be explained by the behavioral changes observed in these animals due to toxicity of oil contamination. An active avoidance of ostracods from the oil treated sediments related to oxygen depletion might have forced them to come out of the sediment and live in the overlying water column to reduce oil exposure (van Eenennaam et al., 2019). According to PERMANOVA, both temperature and oil concentration appeared to have dreadful consequences on the meiofaunal communities (Supplementary Table S1). Harpacticoid copepods are known to be more sensitive than nematodes to pollution (Zeppilli et al., 2015 and references therein). In the present investigation they were virtually absent from the high doses of both the stressors, leaving few individuals sporadically distributed. Thus, absence of copepods in treated benthocosms clearly depicted both the pollution as causative factors. This is consistent with

the findings of [Montagna et al. \(2013\)](#), where abundance of harpacticoids decreased upon an accidental oil spill in the northern Gulf of Mexico.

A spectrum of responses has been noticed on nematofaunal communities against the synergistic effects of stressors. They seem to be resistant at different temperature regimes; notwithstanding to temperature-diesel combination. Occurrence of *Daptonema invagiferoum*, *Sabatieria praedatrix*, *Theristus acer*, *Monhystera* sp. and *Thalassomonhystera* sp. from high temperature + oil treated benthocosms in a good number could be characterized them as 'temperature resistant' or 'diesel resistant' species having higher colonizing potential than other nematode species. Globally these species have been reported as dominant in oxygen-depleted polluted sediments too ([Heip et al., 1985](#); [Schratzberger et al., 2007](#); [Gambi et al., 2009](#)). After oil spillage, the enrichment of these opportunist species might be due to an increased hydrocarbon degrading bacterial population, which serves as food resources for them ([Montagna et al., 2013](#)). On the other hand, *k*-strategists like *Halalaimus gracilis*, *H. longicaudatus*, *Oxystomina aetosa* and *Pomponema* sp. were not recorded from the high temperature and oil amended population in the present observation, which is in accordance with the findings of [Ingole et al. \(2006\)](#). The authors showed that benthic standing stock was not only affected by accidental oil spill of a grounded vessel MV *River Princess*, but also advocated elimination of some oil sensitive species. Hydrocarbon contamination in amalgamation with elevated temperature could be responsible for the mortality of sensitive species than sole effect of temperature as a single stressor. Accumulation of hydrocarbon pollutants in sediments entails depletion of dissolved oxygen and Chl *a* content and are identified as regulating factors for nematode composition ([Neira et al., 2001](#)). Multivariate nematode species-dependent MDS plot also revealed that the response of nematode community was dependent on both the stressors in respect to time. This pattern is in agreement with the observation by [Mahmoudi et al., \(2005\)](#) and [Beyrem et al., \(2007\)](#), where authors found similar results while working with free-living nematode communities in a 90 days mesocosm experiment. The *k*-dominance curves clearly indicated the disturbed nematofaunal assemblage ([Fig. 5](#)). The different patterns of disturbances-induced curves appeared to be due to the lack of nematode genera such as *Halalaimus*, *Oxystomina*, *Oncholaimus* and *Pomponema*. In contrast, other genera, such as *Daptonema*, *Monhystera*, *Sabatieria* and *Theristus* seemed to be tolerant to both kinds of stresses. Thus, our findings reinforced the fact that a decrease in nematode abundance and species composition is a general response to these anthropogenic impacts.

The analysis of nematode life strategies and trophic guilds (in terms of MI and ITD respectively) can be useful to provide further information on anthropic pressures induced impacts on nematode communities ([Meadows et al., 2015](#); [Vafeiadou et al., 2018b](#)). In our experiment, we observed stable values of MI in elevated temperature and oil amended treatments separately because of the occurrence of persistent nematode species suggesting their capacity to cope with stressful environment. Nevertheless, sharp decline in MI values after 30 and 60 days delineated strong synergistic impact as persistent nematode species were unable to survive. Furthermore, species specific responses among nematode communities were observed to cumulative effects of both the contaminants, which might attribute to their divergent stress tolerance potential. We found a shift in the abundance of nematode feeding groups. Overall, non-selective deposit feeding nematodes (1B) maintained their high densities throughout the experiment making the second most abundant group i.e. predators (2B) outnumbered from the competition. The trait characteristics of predators such as larger body size, slow development and low fecundity make them more susceptible to stressors ([Schratzberger and Somerfield, 2020](#)). As larger nematodes are more prone to predation by macrobenthos or higher trophic levels, the elimination of predatory nematodes from meiobenthic population may have detrimental consequences for benthic food web in the context of energy transfer ([Hamerlynck and Vanreusel, 1993](#)). Thus, our results concur

with the hypothesis that intertidal tropical meiobenthic population are more sensitive to elevated temperature due to their narrow thermal tolerance range as well as to higher concentration of hydrocarbon which may differentially alter their population fitness.

Intertidal sediments from tropics naturally experience extreme thermal stress during low tides ([Schneider, 2008](#)). Moreover, due to climate change induced anthropogenic disturbances these shallow marine habitats are subjected to increasing levels of multiple environmental stressors which might alter physiological performances of inhabitants and severely jeopardize their population dynamics. While discussing the impact of oil spill on intertidal benthic assemblages, [Dauvin \(1998\)](#) suggested that hydrocarbon sensitive species played active role in delineating the post spill intertidal faunal communities. When the spilled oil is exposed to sunlight, it becomes more toxic and persistent (photo-enhanced toxicity) resulting in the generation of reactive oxygen species and ultimately inducing tissue damage and mutation of many marine invertebrates inhabiting near shore area ([Alloy et al., 2015](#); [Finch et al., 2016](#)). After photo-oxidation, heavier part of oil generally converted into tar residues (tar balls, tar mats and tar patties) and gradually deposited on the beaches indefinitely, causing massive mortality to beach intertidal organisms ([Warnock et al., 2015](#)). Therefore, hydrocarbon contamination in marine environment, especially in intertidal habitats, can result irreparable damage to marine organisms and thereby affecting socio-economic backbone of coastal population depending on coastal resources for their livelihood. Furthermore, loss or extinction of any species would be detrimental for the health and functioning of the ecosystem. Meiofauna are known to provide ecosystem services being crucial members of benthic food web, consequently any impact on their species composition would perturb several trophic levels and imperil entire benthic community and ecosystem. Moreover it would not suffice to predict the biological consequences of any individual driver in isolation, as many stressors are acting synergistically upon marine biota. Therefore, it is imperative to investigate possible combined effects of multiple stressors on species specific interaction within community structure that have profound repercussion on related benthic trophodynamics.

5. Conclusion

Overall, present study strongly ascertained that climate change induced elevated temperature and hydrocarbon pollution may impair tropical intertidal meiobenthic as well as free-living nematode communities. Our results paint a clear picture, whereby temperature shift coupled with hydrocarbon pollution in the coming decades rapidly and significantly may alter both structural and functional pattern of shallow water benthic biodiversity. Therefore, further multi-stressors based studies are needed to investigate the underlying mechanisms of species-specific resilience and to reveal more embracive knowledge on the interaction between meiofauna and other biota.

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CRediT authorship contribution statement

Moumita Ghosh: Conceptualization, Methodology, Field work, conducting the Experiment, Data analysis, Writing - original draft, Writing - review & editing, Visualization. **Sumit Mandal:** Conceptualization, Methodology, Field work, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.ecoenv.2020.111549](https://doi.org/10.1016/j.ecoenv.2020.111549).

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