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Organic ultraviolet filter mixture promotes bleaching of reef corals upon the threat of elevated seawater temperature

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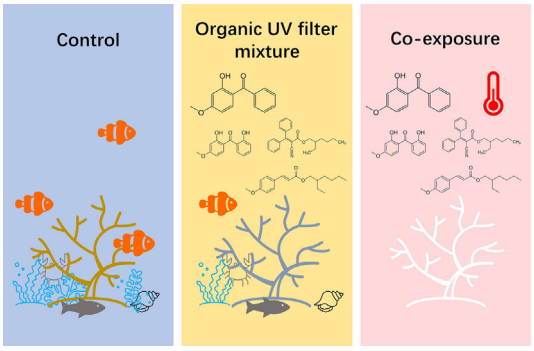
HIGHLIGHTS

- Organic UV filter mixture at environmental concentrations can cause coral bleaching.
- Significant oxidative stress and detoxification burden on corals were induced.
- Effects of organic UV filter mixture were stronger at a higher temperature tested.
- Emerging contaminants may play a unique role in global reef degradation.

GRAPHICAL ABSTRACT



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ABSTRACT

Global reef degradation is a critical environmental health issue that has triggered intensive research on ocean warming, but the implications of emerging contaminants in coral habitats are largely overlooked. Laboratory experiments assessing organic ultraviolet (UV) filter exposure have shown that these chemicals negatively affect coral health; their ubiquitous occurrence in association with ocean warming may pose great challenges to coral health. We investigated both short- (10-day) and long-term (60-day) single and co-exposures of coral nubbins to environmentally relevant organic UV filter mixtures (200 ng/L of 12 compounds) and elevated water temperatures (30 °C) to investigate their effects and potential mechanisms of action. The initial 10-day exposure of *Seriatopora caliendrum* resulted in bleaching only under co-exposure conditions (compounds + temperature). The 60-day mesocosm study entailed the same exposure settings with nubbins of three species (*S. caliendrum*, *Pocillopora acuta* and *Montipora aequituberculata*). Bleaching (37.5 %) and mortality (12.5 %) of *S. caliendrum* were observed under UV filter mixture exposure. In the co-exposure treatment, 100 % *S. caliendrum* and *P. acuta* bleached associating with 100 % and 50 % mortality, respectively, and significant increase of catalase activities in *P. acuta* and *M. aequituberculata* nubbins were found. Biochemical and molecular analyses indicated significant alteration of oxidative stress and metabolic enzymes. The results suggest that upon the adverse effects of thermal stress, organic UV filter mixture at environmental concentrations can cause bleaching in corals by inducing a significant oxidative stress and detoxification burden, suggesting that emerging contaminants may play a unique role in global reef degradation.

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1. Introduction

Coral reefs are some of the most productive and biologically rich ecosystems on the Earth, accounting for an estimated 25 % of all marine life (Burke et al., 2011). They are now under threat from many anthropogenic environmental impacts, such as elevated sea surface temperatures due to global climate change, as well as other human activities such as chemical pollution. These threats have led to reduced areas of living coral, reduced species diversity and lower fish abundance. An approximately 50 % global decline of coral cover was reported as of 2010 (Burke et al., 2011), with an additional 14 % global loss from 2009 to 2018 (Souter et al., 2021). If no effective measures are carried out, all corals in the world will likely be threatened by 2050 (Bindoff et al., 2019). Thus, protection and conservation of coral reefs has become an issue of global importance (United Nations Environment Programme (UNEP), 2017).

Organic UV filters are commonly used in personal care products (PCPs; *e.g.*, sunscreens) to protect skin from the harmful effects of UV radiation such as sunburn and cancers (Santos et al., 2012), and have recently been found to cause stress in reef corals (Downs et al., 2014, 2016; He et al., 2019a, 2019b), including severe bleaching and death at environmentally relevant concentrations. The US state of Hawaii banned sunscreens containing benzophenone-3 (BP-3) and ethylhexyl methoxycinnamate (EHMC) starting in 2021 and the Republic of Palau banned the sale of sunscreens containing any of ten UV filters as active ingredients in 2020, indicating growing concern about the potential risks of organic UV filters to wild corals (McGrath, 2018; Coldwell, 2018). However, UV filters are still widely used in personal care products around the world.

These chemicals enter the aquatic environment mainly through two routes (Diaz-Cruz and Barcelo, 2009): directly through human use of PCPs containing UV filters combined with aquatic recreation (*e.g.*, bathing and swimming), and indirectly *via* wastewater as a result of showering, washing, *etc.* The recommended use of these products is one ounce to evenly cover the whole body with reapplication at least every 2 h (Food and Drug Administration (FDA), 2022). Concentrations of organic UV filters in surface seawater have been reported to range from 2 to 6812 ng/L (maximum: 1,395,000 ng/L), and median levels of approximately 200 ng/L have been reported (Langford and Thomas, 2008; Tsui et al., 2014b; Ramos et al., 2015; Mitchelmore et al., 2021). Higher levels of organic UV filters can usually be measured during warm/wet seasons (2–10 times greater than cold/dry seasons), because sunscreens containing UV filters are often used in large amounts and are often applied shortly before a person enters the water for recreational activities. High levels of organic UV filters have also been found in coral reefs. In Kenting, Taiwan, up to 1 μg/L of organic UV filters, especially BP-3, EHMC, and octocrylene (OC) have been detected in the seawater (Table S1), showing the association between coral reefs and the pollution of organic UV filters. Bioaccumulation of organic UV filters have been found in biota samples such as fish and mussels, generally at levels range from ng/g to μg/g lw (Bachelot et al., 2012; Balmer et al., 2005; Buser et al., 2006; Carve et al., 2021). Our research group conducted the first bioaccumulation study for coral tissue samples, and organic UV filters at ng/g ww levels, particularly benzophenones, have been found in Hong Kong coral reefs, showing that corals are directly exposed to a variety of organic UV filters in the real environment (Tsui et al., 2017). As coral habitats are often located in coastal areas and near beaches, the levels of organic UV filters in the surface seawaters of tropical and subtropical coastal areas could be regarded as representative environmental concentrations of these chemicals in the marine environment in Southeast Asia for coral reefs.

Studies of the toxicities of organic UV filters have mainly focused on human health, such as hormonal effects (Huang et al., 2021). Research on non-target organisms such as corals usually focus on the toxicities of single compounds. Vuckovic et al. (2022) found that BP-3 (2 mg/L) is modified into a potent photosensitizer within coral cells *via* conjugation with glucose. Algal symbionts sequestered these conjugates, and mortality correlated with conjugate concentrations in the coral cytoplasm. Research by Downs et al. (2014, 2016) suggests that BP-2 and -3 are both phototoxic and genotoxic to corals. Our previous studies also indicated that coral exposure to single organic UV filters can cause significant larval settlement failure and bleaching and mortality in adults at relatively high concentrations ($\geq$ 10 μg/L) (He et al., 2019a, 2019b). When considering environmentally relevant concentrations, single BP-3 and 4-MBC exposures at 1.0 μg/L and exposure to a mixture of BP-3, EHMC and OC at 500 ng/L each was able to induce adverse oxidative stress in a protozoan (*Tetrahymena thermophile*) and zebrafish embryos (*Danio rerio*), respectively (Gao et al., 2013; Li et al., 2018). Corals are exposed to a variety of organic UV filters in the environment, and therefore it is of great importance to investigate the potential mixture effects. Mixture and co-stressor effects have also been identified as critical research gaps for understanding the impacts of UV filters in corals (Watkins and Sallach, 2021).

In recent decades, high seawater temperatures have been recorded globally (Bindoff et al., 2019), and are known to be one cause of large-scale coral bleaching in the environment. Coral reefs can recover from infrequent bleaching events, but severe and frequent thermal stress can cause irreversible damage and massive mortality to corals (Burke et al., 2011). In Taiwan, severe mass coral bleaching events occurred in 1998, 2007, and 2016–17 (Chen and Shashank, 2009; Keshavmurthy et al., 2019), and more recently, a severe coral bleaching event associating with a significant mortality was recorded in Kenting, southern Taiwan (Wu and Lin, 2020; Fig. S1 of SI), a popular tourism area where 30 % of all hard coral species are known to occur (Chang et al., 2008). Severe coral bleaching events and decline of reef coverage also associated with abnormally warm seawater temperatures during El Niño events (Chen and Shashank, 2009; Keshavmurthy et al., 2019). In contrast, acclimatization of corals to climate change (*i.e.*, high temperature and acidification) have also been reported in a variety of studies in Kenting, Taiwan (Table 1) (Mayfield et al., 2018; Lee et al., 2020); coral bleaching and mortality were not observed in simulation studies using measured field seawater temperatures over the past decade (Fig. S2 of SI). However, no matter how the development of resistance is going on, the degradation of corals (*e.g.*, *Pocilloporidae*) keeps developing fast (Wu and Lin, 2020; Kuo et al., 2012). These studies imply that coral reefs in Taiwan confront a more complicated situation, and apart from heat exposures, other threats, *e.g.*, chemical pollution, may play a role on the degradation of Taiwan reefs, which have long been ignored in the field studies on bleaching events. Moreover, in hot seasons, when high seawater temperature is likely to occur and may persist for a long period, high levels of organic UV filters are released into seawater due to human recreational activities around the sea beaches and coastal areas. A previous study by Wijgerde et al. (2020) discussed the 6-week chronic impact of a single organic UV filter (BP-3 at approximately 0.06 μg/L) at elevated temperatures (33 °C) to corals and showed that BP-3 exposure can affect coral photosymbionts and alter the coral microbiome. However, the potential effects of co-exposure to a complex organic UV filter mixture at environmentally relevant concentrations and high temperatures to different coral species have not yet been evaluated.

The aim of this study was to assess the effects of combined stressors to corals: a mixture of UV filters at environmental concentrations and elevated temperature. Both short- (10-day) and long-term (60-day) exposures were conducted on coral nubbins to assess the effects of an environmentally relevant organic UV filter mixture alone and co-exposure to the mixture and elevated water temperature (Tables 2, S2, and S3). Effect endpoints included visual bleaching, photosynthetic efficiency, and zooxanthellae density in the short-term study on one species (*S. caliendrum)* (Table S2), with the addition of coral growth, mortality, antioxidant enzyme activities and expression of oxidative stress, reproduction and detoxification genes in the 60-day mesocosm exposure of three species (*S. caliendrum*, *P. acuta*, and *M. aequituberculata)* (Table S3).

2. Materials and methods

2.1. Chemical preparation

Twelve organic UV filters are particularly prevalent in sunscreens sold across the world, where their concentrations range from 3 to 15 % (*w*/w):

Table 1
Bleaching and mortality of adult *S. caliendrum*, *S. hystrix*, *P. acuta*, and *M. aequituberculata* expose to different temperature ranges, high pCO_2, a mixture of organic UV filters, and co-exposure treatments in Kenting, Taiwan. Compared to the exposure conditions, temperature was about 26 °C and pCO_2 was approximately 400 ppm in control treatments. *, data from this study. Data in bold and italic shows the exposure condition of treatment. Percentage of bleaching and mortality was shown at the day when the response was observed. N/A, not available. Other information from Mayfield et al. (2018).

Coral species	Treatment			Period	Parameter	
	Temperature (°C)	pCO_2 (ppm)	UV filters		Bleaching	Mortality
*S. caliendrum**	***30***	N/A	***Yes***	10 days	33.3 %, Day 8	N/A
*S. caliendrum**	25	N/A	***Yes***	60 days	12.5 %, Day 36	12.5 %, Day 60
*S. caliendrum**	***30***	N/A	***Yes***	60 days	12.5 %, Day 6	12.5 %, Day 24
S. hystrix	***23–29 (over 6 h)***	N/A	No	days	N/A	N/A
S. hystrix	***30***	N/A	No	hrs	N/A	N/A
S. hystrix	25	***800***	No	weeks	N/A	N/A
*P. acuta**	25	N/A	***Yes***	60 days	N/A	N/A
*P. acuta**	***30***	N/A	***Yes***	60 days	50 %, Day 18	25 %, Day 48
P. acuta	***29***	***850***	No	weeks	N/A	N/A
P. acuta	***29.7***	N/A	No	252 days	N/A	N/A
P. acuta	***31.5 (return to ambient at night)***	N/A	No	weeks	N/A	N/A
P. acuta	***31.5 (sustained)***	N/A	No	21 days	75 %, Day 14	~80 %, Day 21
P. acuta	25	***800***	No	months	N/A	N/A
P. acuta	***28 or 31***	***800***	No	months	N/A	N/A
P. acuta	***29.5***	N/A	No	months	N/A	N/A
P. acuta	***32***	N/A	No	hrs	N/A	N/A
*M. aequituberculata**	25	N/A	***Yes***	60 days	N/A	N/A
*M. aequituberculata**	***30***	N/A	***Yes***	60 days	25 %, Day 36	N/A

4-methylbenzylidene camphor (4-MBC), butyl methoxydibenzoylmethane (BMDBM), benzophenone-1 (BP-1), benzophenone-3 (BP-3; oxybenzone), benzophenone-4 (BP-4), benzophenone-8 (BP-8), ethylhexyl methoxycinnamate (EHMC; octinoxate), ethylhexyl salicylate (EHS), homosalate (HMS), isoamyl *p*-methoxycinnamate (IAMC), octocrylene (OC), and octyl dimethyl-*p*-aminobenzoic acid (OD-PABA) (Table S4). Recently, these twelve organic UV filters have been detected in the surface water of many popular recreational areas of Kenting, Hong Kong, Japan and other countries and regions. Thus, an equimolar mixture of twelve organic UV filters was prepared at a concentration of 200 ng/L. In these experiments, methanol was used as solvent for these chemicals and in the solvent control because it had no significant toxicity in previous exposure experiments (He et al., 2019a, 2019b) and is an effective solvent for structurally diverse organic UV filters. Additional information on chemicals can be found in the SI.

2.2. Coral species, colony collection and sample preparation

Three subtropical and tropical coral species, *S. caliendrum*, *P. acuta*, and *M. aequituiberculata*, were chosen for this study. They are common coral species in the Coral Triangle, which is sited in an area of Southeast Asia and the Western Pacific and is named due to the shape of its ecological boundary and the highest diversity of corals worldwide (76 % of all known coral species).

An official permit authorized by Kenting National Park Headquarters (No. 1030002637) was obtained for coral collection in Kenting National Park in southern Taiwan, while the number of coral colonies and the seasons for collection were scheduled subject to the distribution and condition of the wild corals and arrangements made by the Kenting National Park Headquarters. Intact colonies were detached from the reef in Hobihu, Nanwan, Kenting National Park of southern Taiwan (21°56′18.01″N, 120°44′45.54″E) and were quickly transported to the husbandry center of the National Museum of Marine Biology and Aquarium, Taiwan (NMMBA) (Fig. S1 of SI). Healthy coral colonies with dark-colored external tissues, pure white skeleton, polyps sensitive to touch (but re-opening within ~1 min) were used in this study. Coral fragments (about 3 g) were prepared and allowed to recover in seawater under indoor conditions [flow-through water recycling, natural photoperiod (usually from 6:30 am to 5:30 pm during the experiments), ambient temperatures (23–25 °C); Putnam et al., 2010] for recovery. Detailed information about the seawater quality for culture and exposure is provided in the SI. After two months, healthy fragments that had completely recovered were employed for tests.

2.3. 10-day exposure

The settings of the exposure were similar to those described in our previous studies with some modifications (He et al., 2019a, 2019b). Nubbins (n = 6 for each treatment) were exposed to treatments of (A) the organic UV filter mixture (an equimolar mixture of 12 UV filters at 200 ng/L) at normal temperature; (B) elevated temperature (30 °C) alone; and (C) co-exposure of the organic UV filter mixture and elevated temperature. Blanks and solvent controls (0.01 % methanol) at 25 °C were also included

Table 2
Treatments and parameters in the 10-day exposure and in the 60-day mesocosm study. The **α**, **β**, and **γ** treatments in the 60-day exposure align with those of **SC**, **A**, and **C** in the 10-day exposure, respectively. 10-day exposure: three bottles per treatment, two nubbins per bottle, measurements made on individual nubbins (n = 6); 60-day exposure: 40 nubbins of *S. caliendrum*, 50 nubbins of *P. acuta*, and 40 nubbins of *M. aequituiberculata* per mesocosm, measurements made on individual nubbins. More information about physicochemical parameters measured can be found in the **Table S2** and **S3**. BC, blank control; SC, solvent control.

10-day exposure	Treatments Conditions	**BC**	**SC**	**A**	**B**	**C**	**Parameters**
	Solvent control	–	✓	–	–	–	Bleaching (n = 6, daily), photosynthetic efficiency (n = 6, once every 2 days)
	UV filter mixture + Solvent	–	–	✓	–	✓	and zooxanthellae density (n = 3, Day 10)
	Temperature (°C)	25	25	25	30	30	
60-day mesocosm study	Treatments Conditions	–	**α**	**β**	–	**γ**	**Parameters**
	Solvent control	–	✓	–	–	–	Mortality and bleaching (n = 8, daily), photosynthetic efficiency
	UV filter mixture + Solvent	–	–	✓	–	✓	(n = 8, once every two days), zooxanthellae density and enzyme activities
	Temperature (°C)	–	25	25	–	30	(n = 4, Day 1, 4, 7, 14, 30, and 60), growth (n = 4, Day 0, 14, 30, and 60), and gene expression (n = 4, Day 1, 4, 7, 14, 30, and 60, for *P. acuta* only)

(Table S2). Nubbins were exposed in 800 mL seawater in glass bottles with two *S. caliendrum* nubbins in each bottle and three bottles in each treatment containing (*i.e.*, $n = 6$). To satisfy the irradiation needs of the corals under changing natural sunlight levels, natural sunlight and artificial light with a full spectrum similar to sunlight were employed (14:10 light:dark cycle and 200–300 μmol quanta m^{-2} s^{-1} irradiance (photosynthetically active radiation)). For the exposures, salinity, temperature, pH and dissolved O_2 were tested and maintained daily, 50 % of the seawater was renewed once every two days, and aeration was provided. The selected stressor temperature of 30 °C is a bit higher than the range of normal temperature (about 20–28 °C; 25 °C in this study) in which corals live in Kenting, Taiwan. The temperature of the bottles was maintained using a separated water bath with heaters (Decdeal, Japan).

2.4. 60-day mesocosm exposure

Three treatments were set up (Table S3; Fig. S3 of SI), including the solvent control (α), the organic UV filter mixture exposure at normal temperature (25 °C) (β), and the organic UV filters mixture with elevated temperature (30 °C) (γ). This exposure did not include a blank treatment or high-temperature treatment to reduce the number of corals nubbins needed. Moreover, the 10-day exposure and our previous studies (Mayfield et al., 2013a, 2013b) have been conducted to evaluate the effects of elevated temperature on corals in Kenting, Taiwan (Table 1).

The settings of the present mesocosm study were similar to those described in our previous studies with some modifications (Mayfield et al., 2013a, 2013b). 500 L tanks set indoors with a glass roof blocked by blue and semitransparent woven polypropylene cloth and with open walls were used for the mesocosms. All exposure tanks were lined with polytetrafluoroethylene (PTFE) sheets to prevent sorption of the UV filters to tank surfaces. The PTFE sheets were soaked in seawater for one week prior to use, and the water was collected and tested to determine whether the sheets contained the targeted organic UV filters. The tanks were equipped with pumps to create current and temperature controllers (2 water heaters of 500 W per tank). The bottom of the tanks was paved with coral skeleton sands. Three gobies (*Istigobius ornatus*), two sea snails (*Tectus spp.*), and three clown fish (*Amphiprion spp.*) were added into each tank to stimulate real conditions. Fish food was provided twice per day, and coral food was provided once every three days. The amount of food (*Artemia*) to be provided was calculated based on the total weight of fish and coral nubbins at the beginning of the exposure.

Seawater from a reservoir pool where many coral nubbins were being cultured was stored in two large tanks (500 L and 1000 L) and filtered using a sand water filter system consisting of sand, ceramic sand, and artificial sponges before use. Temperature in the tanks was measured by HOBO® pendant data loggers (Onset, MA, USA). At least three coral nubbins of each species were put in each tank for at least 3 days to test the quality of the fresh seawater before the initiation of the exposures. For the experiments, corals were hung from transparent support structures and immersed in water to allow for easy observation and sample collection (Fig. S3 of SI), and 40 nubbins of *S. caliendrum*, 50 nubbins of *P. acuta*, and 40 nubbins of *M. aequituiberculata* were used per mesocosm. Seven days' adaption was conducted before the experiments. Half of the seawater volume was renewed every three days, and the mixture was added to the tanks after water renewal. Solvent concentrations in the tanks were approximately 0.00002 %. The exposure lasted for 60 days. Physicochemical parameters, pH, dissolved oxygen, salinity, and temperature of the seawater in the tanks, were measured daily. The light intensity was measured daily at 9:00, 11:00, 13:00, 15:00 and 17:00. To avoid too much intrusion and disturbance, the light intensity was only measured for the level above the seawater surface. The level of light intensities in the seawater for each coral nubbin was maintained to a similar degree, but the actual reading of the light intensities was subject to the outdoor sunlight intensity. In addition, to maintain the salinity of the seawater in the tank, distilled water was added little by little when necessary.

2.5. Chemical analysis

Chemical analysis was only carried out for the 60-day mesocosm study. Every 6 days, 1 L seawater in each treatment were collected and stored at −20 °C soon after water renewal. Chemical analysis for water samples was performed according to the method described in Tsui et al. (2014a) and He et al. (2019a, 2019b), in which solid phase extraction and high-performance liquid chromatography-electrospray ionization-tandem mass spectrometer were applied. Bioaccumulation of organic UV filters in coral tissues (Day 60, $n = 6$) were detected according to the method developed by Tsui et al. (2017). Briefly, coral samples were freeze-dried and ground into fine particles, and then extracted with a hexane:acetone solution and blown by gentle stream of N_2 to dryness. The extract was reconstituted with methanol, spiked into MilliQ water in a glass bottle, and stored at 4 °C overnight. The rest of the procedures was the same as that for water samples. This method is not applicable for the extraction of BMDBM, BP-4, EHS, HMS, and IAMC in coral tissue, so concentrations of these compounds are not reported in this study. The procedural recoveries and measured limits of detection (MLODs) of compound in water and tissue samples are shown in Table S5. Bioaccumulation factors (BAFs; Day 60) of the nubbins of three coral species were calculated based on the equations below:

$$\mathrm{BAFs} = \frac{\text{Concentration of toxicant in tissue (ng/g dw)}}{\text{Concentration of toxicant in water (ng/mL)}}$$

2.6. Parameters

Parameters in the 10-day exposure and in the 60-day mesocosm study are shown in Table 2. Briefly, bleaching ($n = 6$, daily), photosynthetic efficiency (n = 6, once per 2 days) and zooxanthellae density ($n = 3$) measurements were carried out for 10-day exposure, while mortality ($n = 8$, daily), bleaching (n = 8, daily), photosynthetic efficiency (n = 8, once per two days), zooxanthellae density ($n = 4$, Day 1, 4, 7, 14, 30, and 60) and growth (n = 4, Day 0, 14, 30, and 60) were measured for the mesocosm study. Measurements for these parameters were performed according to the methods described by Putnam et al. (2010), Marsh (1970) and He et al. (2019a, 2019b). Additional information for the methods is provided in the SI. For the tests of growth, coral nubbins were buoyantly weighed in a chamber under a balance (W0, weight of nubbins at Day 0) prior to experimentation (Davies, 1989). At each time point, nubbins were re-weighed to calculate growth. Growth rate was normalized to number of days passed or to W0.

Antioxidant enzyme activities of superoxide dismutase (SOD) and catalase (CAT) of three coral species were tested ($n = 4$, Day 1, 4, 7, 14, 30, and 60) for the mesocosm study. Protein of coral samples was extracted with buffer (500 mM sucrose, 1 mM EDTA, 10 mM Tris-HCl, pH 7.4) using the force of homogenization (30,000 ×, LabGEN™ 7, Cole-Parmer, USA). Protein concentration was also tested for the normalization of the data obtained in the enzyme activities tests according to the method developed by Bradford (1976). The activities of SOD and CAT were tested with the methods provided in commercial kits (Superoxide Dismutase Assay Kit (Item No. 706002) and Catalase Assay Kit (Item No. 707002; Cayman Chemical, Michigan, USA).

Measurement of gene expression was conducted for the mesocosm study by using the method developed by Mayfield et al. (2013b). For the evaluation of oxidative stress, the gene expression of *symbiodinium* ferric manganese SOD (FeMnSOD, S-*fsod*), copper zinc SOD (CuZnSOD, S-*csod*) and catalase peroxidase (Kat-G, S-*kat-g*), host FeMnSOD (P-*fsod*), CuZnSOD (P-*csod*) and CAT (P-*cat*) were analyzed. Expression of vitellogenin-1 (VTG-1, P-*vtg*) and CYP P450 1A1 (CYP1A1, P-*cyp1a1*) genes were also studied. Primers for each gene were designed according to related gene sequences (Table S6) and the primer efficiency of each pair of primers was tested. At Day 1, 4, 7, 14, 30 and 60, *P. acuta* coral nubbin samples (about 30–50 mg) were collected ($n = 4$). Total RNA of the samples was extracted by the TRIzol extraction method (Invitrogen) and were reverse transcribed and used for the real-time PCR assays. A Solaris™ RNA Spike Control Kit (Dharmacon, GE healthcare life Sciences, Little Chalfont, UK) was used to spike into RNA extracts for the gene expression normalization (2013b).

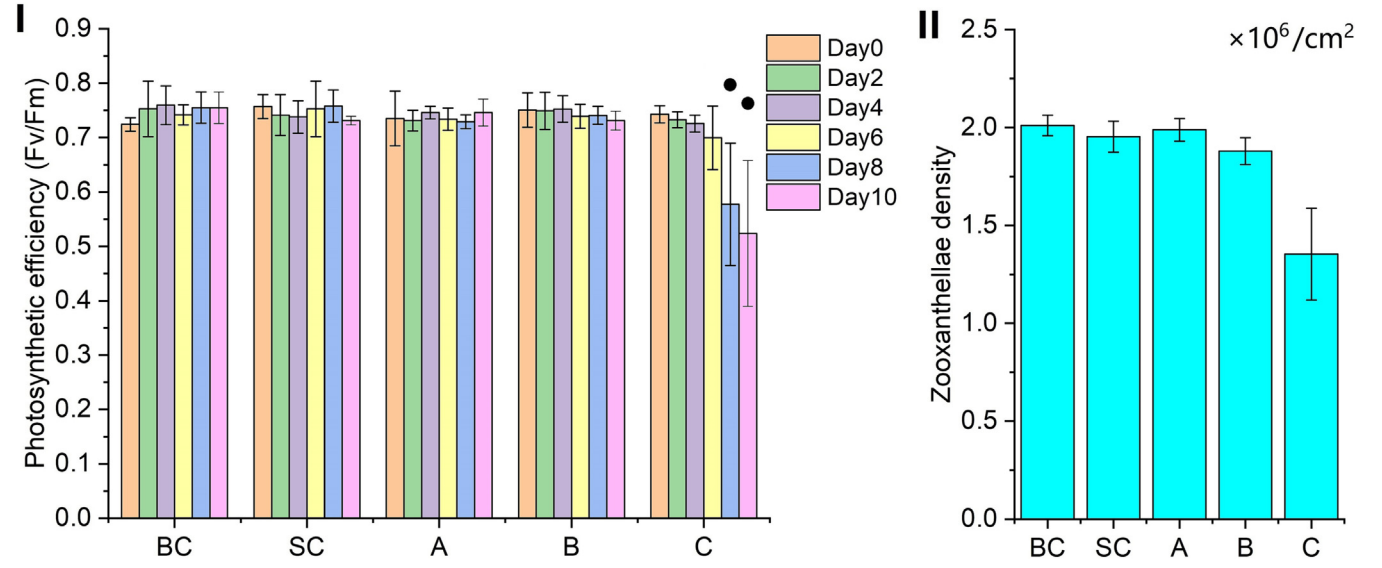

Fig. 1. (**I**) Photosynthetic efficiency (Kruskal-Wallis, $H_{29,180} = 52.068$, $p < 0.01$) and (**II**) zooxanthellae density (Kruskal-Wallis) of *S. caliendrum* measured in the 10-day exposure. Treatments of the 10-day exposure include: (A) organic UV filter mixture (12 UV filters with each at 200 ng/L) at normal temperature; (B) elevated temperature, 30 °C; (C) co-exposure of organic UV filter mixture and elevated temperature, and with blank (BC) and solvent (SC) controls at 25 °C. Bleaching (50 %) of *S. caliendrum* nubbins was only observed in Treatment C (**Fig. S6 of SI**). Compared with blank control, ●, $p < 0.01$.

Zooxanthellae density was also used to normalize the expression of *Symbiodinium* genes as follows:

$$\text{Zooxanthellae density ratio} = \frac{\text{Zooxanthellae density of each sample}}{\text{Zooxanthellae density of a sample (fixed)}}$$

$$\text{Normalized data} = \frac{\text{Gene expression data of each gene of each sample}}{\text{Zooxanthellae density ratio}}$$

2.7. Data analysis

Data are expressed as mean ± standard deviation. For statistical analysis, Mann-Whitney two-sample statistic, one-way ANOVA (Factor: dose), or Repeated Measures ANOVA [Factors: (i), day and (ii), dose (or treatment)]. An analysis of whether there is an interaction (iii) between (i) and (ii) on the dependent variable was also included and *post hoc* Duncan's test ($\alpha = 0.05$) were conducted using IBM SPSS Statistics 20 (IBM Corporation, USA). Figures were plotted by using SigmaPlot 12.5 (Systat Software Inc., USA) and Origin 2018 (OriginLab Corporation, USA). For the enzyme activities and gene expression tests, data gained before the bleaching occurred were analyzed separately.

3. Results and discussion

Previous studies showed that single doses of organic UV filters (*e.g.*, BP-1, BP-2, BP-3, BP-8) caused coral bleaching and mortality at levels ≥10 μg/L (Downs et al., 2014, 2016; He et al., 2019a, 2019b). In the present study, mesocosm exposure to a mixture of 12 organic UV filters at time-weighted average concentrations ranging from 100 to 270 ng/L (Figs. S4 and S5 of SI) caused mortality (12.5 %) and bleaching (37.5 %) (Figs. 2 and S7 of SI) of *S. caliendrum* nubbins from Day 36. The addition of thermal stress to the exposure conditions caused significant effects on bleaching (50 %) of *S. caliendrum* from Day 8 in the 10-day exposure (Figs. 1 and S6

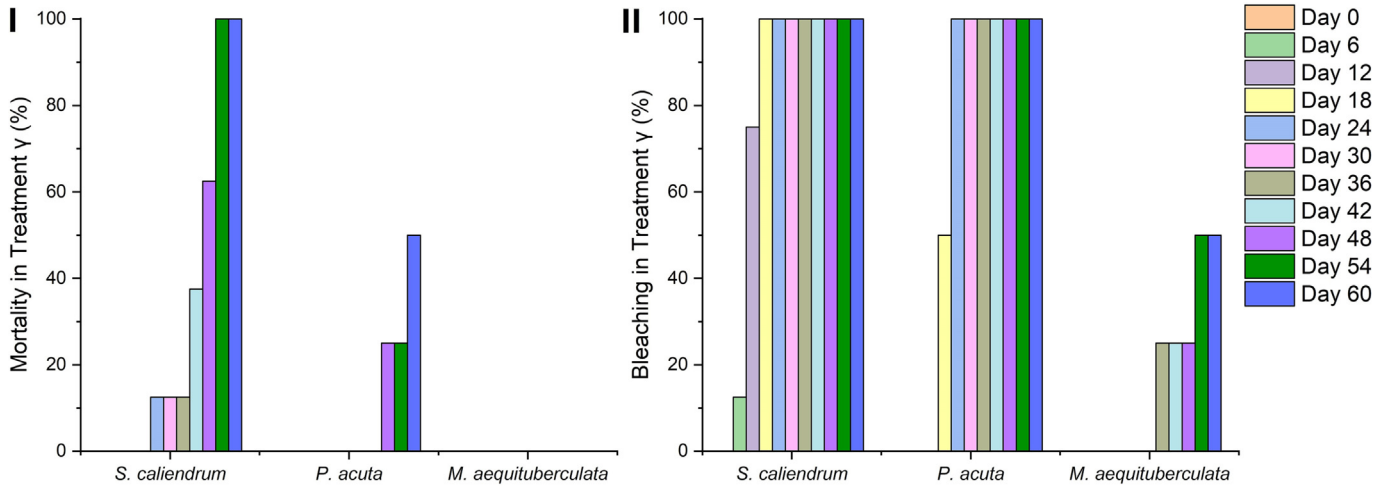

Fig. 2. (**I**) Mortality (%) and (**II**) Bleaching (%) of *S. caliendrum*, *P. acuta*, and *M. aequituberculata* observed in Treatment γ [the UV filter mixture (12 UV filters each at 200 ng/L) and elevated temperature (30 °C) co-exposure treatment] of the 60-day study ($n = 8$). No mortality and bleaching of coral nubbins were observed in the solvent control (25 °C), while mortality (12.5 %) and bleaching (37.5 %) of *S. caliendrum* nubbins were observed in UV filter mixture only treatment (**Fig. S7 of SI**). No mortality of *M. aequituberculata* was observed in all the treatments.

of SI) and caused overall 83.3 % bleaching and 50 % mortality on the nubbins of three coral species in the mesocosm exposure (Figs. 2 and S7 of SI), suggesting a significant impact of the co-exposure to corals. It is worth noting that single thermal stress treatment (*i.e.*, 30 °C) did not cause severe bleaching and mortality of corals in short-term and long-term exposures in previous studies and the present study (Table 1). The results of the present study showed that organic UV filters exposure can lead to severe impacts on vulnerable corals (*e.g.*, *S. caliendrum*), while the combination of organic UV filter exposure and thermal stress led to coral bleaching and mortality, showing that the effects of UV filters were stronger at the higher temperature tested.

Photosynthetic efficiency and zooxanthellae density (Figs. 3, S8 and S9 of SI) were also significantly impacted in *S. caliendrum* in both the UV filter mixture treatment and the UV filter-temperature co-exposure (treatments β and γ, respectively), and in *P. acuta* and *M. aequituberculata* in Treatment γ. These results were in accord with the growth rate results of these three coral species (Figs. 3 and S10 of SI). The growth of coral hosts relies heavily on the sugars generated *via* photosynthesis of their symbiotic zooxanthellae (Dustan, 1999; Stone et al., 1999). In the present study, significant impacts on *P. acuta* were found in Treatment γ from Day 14 to Day 60, while the photosynthetic efficiency and zooxanthellae of these nubbins decreased dramatically (by approximately 9–100 %) during this period, and significant impacts on photosynthetic efficiency and zooxanthellae density were found from Day 24 and Day 30 onward, respectively. Similar results were also found in treatments β and γ of *S. caliendrum*. The decrease of photosynthetic efficiency and zooxanthellae density likely results in a large reduction in the corals' energy reserves, and the growth of the nubbins was severely impacted.

Strong negative effects of an organic UV filter mixture and thermal stress to corals in terms of oxidative stress have been evidenced through molecular analyses (Figs. 4 and S11-S16 of SI). SOD (including CuZnSOD and FeMnSOD) is a key enzyme to catalyze the dismutation of the superoxide radical into hydrogen peroxide and molecular oxygen, while CAT and Kat-G are mainly involved in the degradation of hydrogen peroxide. The imbalance between reactive oxygen species (ROS) and antioxidant enzymes leads to oxidative stress. The increase of the expression and activities of antioxidant enzymes in organisms means that excess ROS are generated, and oxidative stress has occurred (Birben et al., 2012). SOD activity of

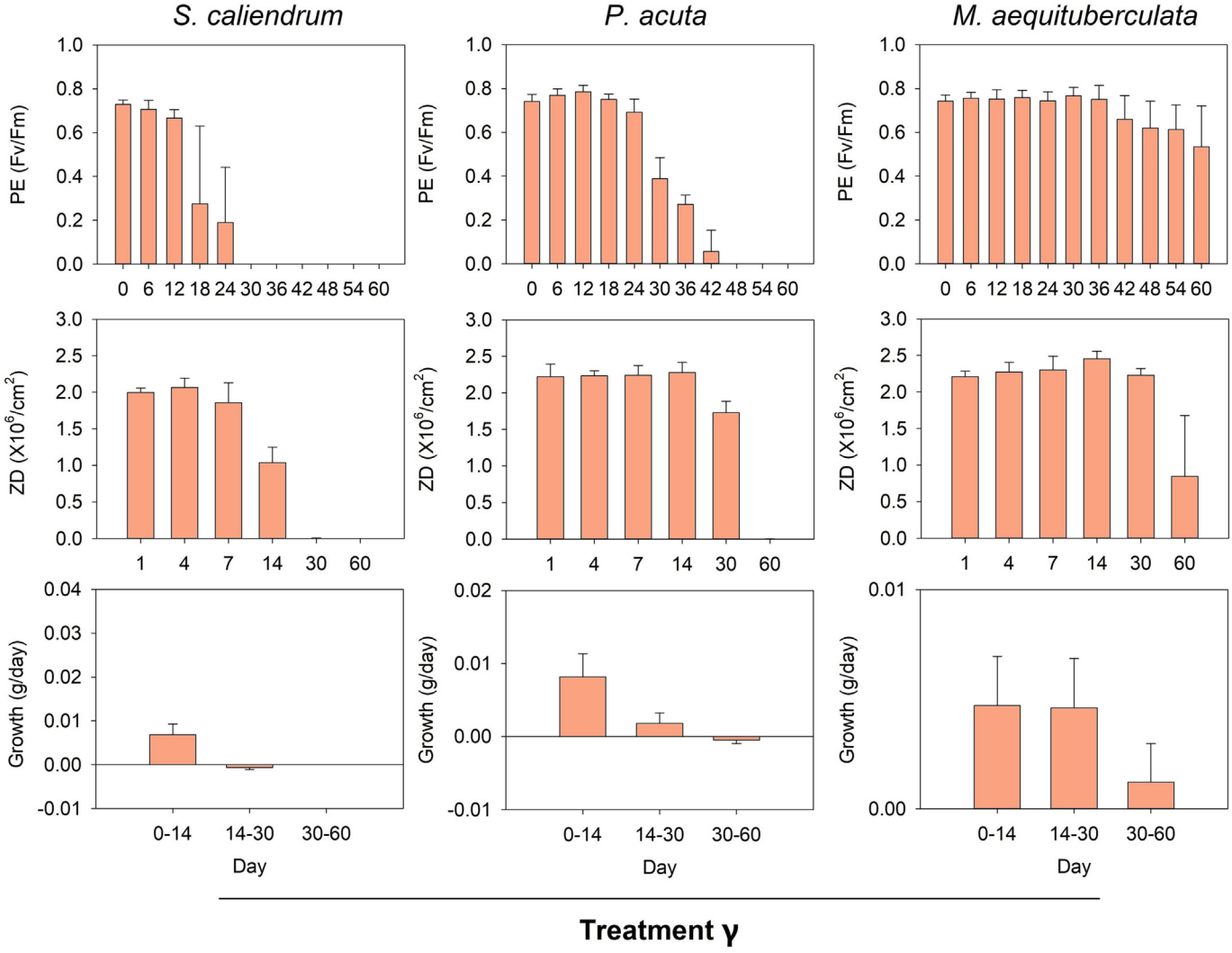

Fig. 3. Photosynthetic efficiency (PE, unit: Fv/Fm, n = 8) of *S. caliendrum* (Kruskal-Wallis, significant effects were observed from Day 12), *P. acuta* (Kruskal-Wallis, significant effects were observed from Day 24) and *M. aequituberculata* (Kruskal-Wallis, significant effects were observed from Day 42); zooxanthellae density (ZD, unit: $\times 10^6/cm^2$, n = 4) of *S. caliendrum* (Kruskal-Wallis, significant effects were observed from Day 14), *P. acuta* (Kruskal-Wallis, significant effects were observed from Day 30) and *M. aequituberculata* (Kruskal-Wallis); and growth rate (normalized to number of days, unit: g/day, n = 4) of *S. caliendrum* (Kruskal-Wallis, significant effects were observed at Day 0–14 and 14–30), *P. acuta* (Kruskal-Wallis, significant effects were observed at Day 14–30 and 30–60) and *M. aequituberculata* (Kruskal-Wallis) measured in Treatment γ of the 60-day study. Only the results in Treatment γ were shown, and more detailed information was provided in **Figs. S8-S10 of SI**. No significant changes were measured in Treatment α. Treatments of the 60-day exposure include: (α) solvent control at normal temperature 25 °C; (β) organic UV filter mixture (12 UV filters with each at 200 ng/L) at 25 °C; (γ) co-exposure of organic UV filter mixture and elevated temperature 30 °C.

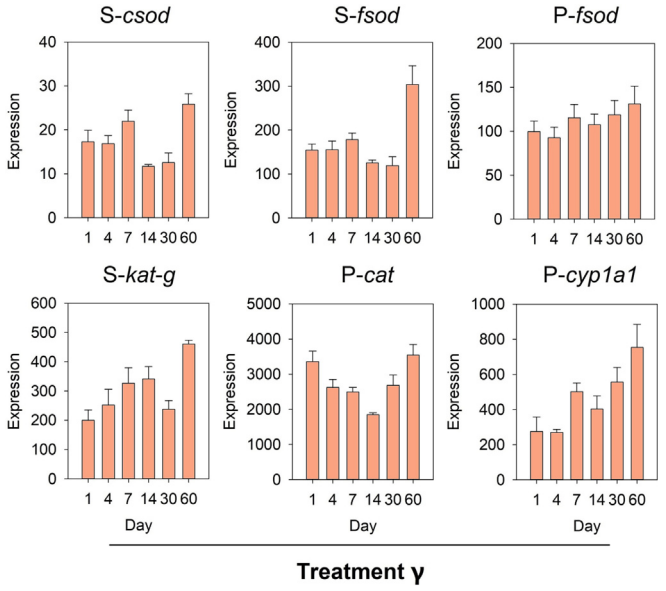

Fig. 4. Expression of *Symbiodinium* CuZnSOD (S-*csod*) (Kruskal-Wallis, significant effects were observed at Day 7, 14, and 60) ($n = 4$); expression of *Symbiodinium* FeMnSOD (S-*fsod*) (Kruskal-Wallis, significant effects were observed at Day 4, 7, 14, and 60) (n = 4); expression of host FeMnSOD (P-*fsod*) (Kruskal-Wallis, significant effects were observed at Day 1, 14, and 60) (n = 4); expression of *Symbiodinium* Kat-G (S-*kat-g*) (Kruskal-Wallis, significant effects were observed at Day 7, 14, and 60) (n = 4); expression of host CAT (P-*cat*) (Kruskal-Wallis, significant effects were observed at Day 1, 4, 7, 30, and 60) (n = 4); and expression of host CYP1A1 (P-*cyc1a1*) (Kruskal-Wallis, significant effects were observed at Day 4, 7, 14, 30, and 60) (n = 4) in Treatment γ of the 60-day study. Only the results in Treatment γ were shown, and more detailed information was provided in **Figs. S15 and S16 of SI**. No significant changes in expression were observed in the solvent control. Treatments of the 60-day exposure include: (α) solvent control at normal temperature 25 °C; (β) organic UV filter mixture (12 UV filters with each at 200 ng/L) at 25 °C; (γ) co-exposure of organic UV filter mixture and elevated temperature 30 °C.

S. caliendrum (Figs. S11 and S13 of SI) and the expression of host CAT of *P. acuta* (Figs. S15 and S16 of SI) increased significantly before bleaching occurred in the organic UV filter treatment when compared with the control. Particularly, SOD activity in *S. caliendrum* was significantly upregulated in Treatment β from Day 14 (Figs. S11 and S13 of SI) to the beginning of the decrease of photosynthetic efficiency and bleaching (Day 36) (Figs. S7 and S8 of SI), showing that the significant oxidative stress occurring during this period is one of the factors leading to the bleaching and mortality of *S. caliendrum*. Treatment γ upregulated the activities of *P. acuta* CAT and *S. caliendrum* SOD and the expression of host FeMnSOD, *symbiodinium* CuZnSOD, FeMnSOD, and Kat-G before bleaching occurred when compared with treatments α and β (Figs. 4 and S11-S16 of SI). Notably, the expression of host FeMnSOD, CAT and *symbiodinium* Kat-G in Treatment γ was upregulated from the beginning of the exposure (Day 1–7) (Figs. 4, S15 and S16 of SI), and the bleaching of *P. acuta* occurred from Day 18 (Figs. 2 and S7 of SI), showing that the persistent oxidative stress caused by this co-exposure over time underlies the bleaching and mortality of *P. acuta*. Moreover, the mortality of *P. acuta* was found from Day 48 in Treatment γ (Week 6–7) (Figs. 2). Our previous study showed that *P. acuta* collected from the same site as the present study were found to have survived a 36-week exposure to 30 °C in an indoor mesocosm study (Mayfield et al., 2013b), while in another mesocosm study, continuous exposure to 31.5 °C caused 75 % bleaching of corals at Day 14 and ~80 % mortality at Day 21 (Mayfield et al., 2013a) (Table 1). These results showed that *P. acuta* in Kenting, Taiwan, can balance the excess ROS generated under thermal stress (*e.g.*, 30 °C) exposure for a long period, but the balance can be tipped by either 1–2° higher of temperature or other type of stressors, *e.g.*, organic UV filters at environmental concentrations. Many studies have reported that thermal stress and chemicals (*e.g.*, Irgarol 1051) cause oxidative stress on corals and finally lead to bleaching and mortality (Downs and Downs, 2007; Downs et al., 2016; Jones and Kerswell, 2003), and oxidative stress has been suggested to be a principal mechanism for coral bleaching and even mortality. Studies by Gao et al. (2013), Li et al. (2018), and Liu et al. (2015) also pointed out that oxidative stress plays a critical role in the toxicities of single or a mixture of UV filters at environmental relevant concentrations to organisms. These results indicate that organic UV filters potentially add insults to corals in the real environment by inducing oxidative stress and thus promote the vulnerability of reef corals to cope with elevated seawater temperature.

The expression of CYP1A1 was also significant upregulated in both treatments β and γ in *P. acuta* (Figs. 4, S15 and S16 of SI). CYP1A1 is a member of the CYP P450 superfamily of enzymes involved in the metabolism of endogenous and exogenous chemicals (Gonzalez, 2005; Liska, 1998). If CYP P450 enzymes are not able to metabolize stable and toxic xenobiotics (*e.g.*, dioxins), these chemicals may accumulate in tissues and cause toxic effects (Nagayoshi et al., 2015; Wheeler et al., 2014). CYP enzymes may also produce metabolites that are more toxic than the original molecule but cannot be eliminated from tissues, which may cause further toxicity (Liska, 1998; Vermeulen, 1996). The upregulation of CYP1A1 expression of *P. acuta* in Treatment β suggests that organic UV filters induce the detoxification activities of CYP1A1, and these activities were intensified by the co-exposure in Treatment γ. At present, there are no data on induction of CYP1A1 or other P450 enzymes by organic UV filters. Our previous study indicated that BP-1 and BP-8 were generated as the metabolites in the BP-3 treatments and accumulated in coral tissue in both laboratory and field, but BP-1 and BP-8 are more toxic than BP-3 at the same concentrations, implying that the metabolic pathway of organic UV filters was functional, but is the presence of an effective elimination pathway is unknown (He et al., 2019b; Tsui et al., 2017).

Species differences in tolerance were observed in the present study, with relative tolerance ranked as: *M. aequituberculata* > *P. acuta* > *S. caliendrum*. One reason for these differences in tolerance may be that both *S. caliendrum* and *P. acuta* are branching coral species, but *M. aequituberculata* is a foliate coral species. Previous studies reported that branching coral species were more severely affected by seawater warming, acidifying, and UV filter exposure than other coral species (Davies et al., 1997; Bahr et al., 2016; Miller et al., 2022). Our previous studies also showed that *P. acuta* is more tolerant than *S. caliendrum* to exposure to organic UV filters, which may be due to higher biodegradation and bioaccumulation capacities for organic chemicals in *P. acuta* (He et al., 2019b). The observed differences in the tolerance of the three coral species to environmental stressors may be ascribed to the diversity of their survival strategies. *M. aequituberculata* and *P. acuta* have conservative survival strategies in that they grow at relatively low rates. In Treatment α (normal conditions), the 60-day growth rates (normalized to W0; Fig. S10 of SI) of *S. caliendrum*, *P. acuta* and *M. aequituberculata* nubbins were 0.81 ± 0.15, 0.32 ± 0.13 and 0.27 ± 0.06, respectively. These results show that *S. caliendrum* and *P. acuta* may allocate more energy and resource to growth than *M. aequituberculata*, while *M. aequituberculata* may allocate more energy and resources to self-defense. Similarly, in a study by Neudecker (1981), *Porites andrewsi*, which grows slower than *P. damicornis* and *Acropora formosa*, had a much higher tolerance to thermal stress (28.5 °C) than faster-growing species and survived for the entire experimental period (>10 weeks). Studies have also reported that fast-growing coral species produce less potent mesenterial filaments and allelochemicals than the slower-growing species in competing for space with neighbors, implying that faster-growing corals may allocate less energy and resources for self-defense (Sutherland et al., 2004). A study by Guest et al. (2012) hypothesized that corals in regions subject to more variable temperature regimes are more resistant to thermal stress than those in less variable environments. In fact, *M. aequituberculata* and *P. acuta* are both common coral species in the Coral Triangle, but *M. aequituberculata* is the only species of the tested corals that also inhabits Hong Kong waters. *S. caliendrum* is found in the Coral Triangle but is only locally abundant in

Table 3
Tissue concentrations (conc., ng/g dw; mean ± standard deviation) of organic UV filters and their bioaccumulation factors (Log_{10}BAFs; mean ± standard deviation) measured on Day 60 of the mesocosm study (n = 6). *S. c.*: *S. caliendrum* nubbin; *P. a.*: *P. acuta* nubbin; *M. a.*: *M. aequituberculata* nubbin.

Treatment	Species	Data	BP-1	BP-3	BP-8	EHMC	OC	4-MBC	OD-PABA
β	***S. c.***	Conc.	5.26 ± 2.15	13.57 ± 3.17	18.21 ± 8.12	17.63 ± 3.75	39.27 ± 12.25	22.39 ± 7.14	14.78 ± 8.09
		Log_{10}BAFs	1.55 ± 0.15	1.90 ± 0.11	1.92 ± 0.20	2.19 ± 0.09	2.26 ± 0.17	2.08 ± 0.14	2.17 ± 0.26
	P. a.	Conc.	6.06 ± 1.96	18.64 ± 9.75	23.36 ± 11.03	20.17 ± 5.97	37.42 ± 13.59	36.90 ± 14.52	14.13 ± 4.92
		Log_{10}BAFs	1.62 ± 0.13	1.97 ± 0.29	2.01 ± 0.24	2.24 ± 0.13	2.24 ± 0.15	2.28 ± 0.17	2.20 ± 0.16
	M. a.	Conc.	5.68 ± 2.19	21.29 ± 7.85	37.52 ± 19.32	23.92 ± 3.94	46.91 ± 10.59	34.39 ± 13.69	18.81 ± 3.16
		Log_{10}BAFs	1.58 ± 0.17	2.07 ± 0.18	2.22 ± 0.24	2.33 ± 0.08	2.36 ± 0.10	2.25 ± 0.20	2.35 ± 0.07
	Mean	Conc.	5.67 ± 0.33	17.83 ± 3.20	26.37 ± 8.17	20.57 ± 2.58	41.20 ± 4.11	31.23 ± 6.33	15.90 ± 2.07
		Log_{10}BAFs	1.58 ± 0.03	1.98 ± 0.07	2.05 ± 0.12	2.25 ± 0.06	2.29 ± 0.05	2.20 ± 0.09	2.24 ± 0.08
γ	***M. a.***	Conc.	2.06 ± 1.51	5.03 ± 1.46	7.45 ± 1.59	10.68 ± 5.83	11.12 ± 4.66	11.07 ± 6.51	6.87 ± 2.11
		Log_{10}BAFs	0.99 ± 0.49	1.49 ± 0.15	1.54 ± 0.10	1.74 ± 0.79	1.66 ± 0.35	1.76 ± 0.21	1.90 ± 0.13

regions like Kenting, Taiwan. According to the Köppen-Geiger system (Peel et al., 2007; World Weather Online (WWO), 2012a, 2012b), Hong Kong (Cfa) has a wider climate temperature range than Kenting (Am). Therefore, corals living in Hong Kong waters are likely to be more tolerant of fluctuating environmental conditions and stressors than corals living in more stable conditions. Overall, the different coral types, survival strategies, and regional adaptabilities likely shape the observed disparities in sensitivity of corals to environmental threats.

The rank of the concentrations and BAFs of organic UV filters to coral tissues are close to the rank of their octanol-water partition coefficients (Table 3 and S4). The concentrations of organic UV filters and BAFs in *M. aequituberculata* were gradually higher than in *P. acuta* and *S. caliendrum* in Treatment β, showing that *M. aequituberculata* has high bioaccumulation capacities to organic UV filters under exposure. The overall BAFs of organic UV filters to corals were also close to the field-measured data in the study of Tsui et al. (2017), showing that the chemical concentrations in tissue may have reached an equilibrium after the 60-day exposure period and the exposure can be persistent in the environment. The long-term adverse effects of organic UV filters to corals in the real world should be of great concern.

4. Conclusion

In recent decades, corals are under threat from many anthropogenic environmental impacts and severe coral reef declines have been documented globally, including in Taiwan. In this study, co-exposure of organic UV filter mixture at environmentally relevant concentrations and elevated temperatures to common reef coral species led to significant detrimental impacts; these negative effects were not observed in the elevated temperature treatment. These results reflect the potential role of emerging contaminants in reducing the capacity of corals to cope with aspects of climate change and in accelerating reef degradation. Management and conservation of coral reefs must take environmental pollution and co-exposure into consideration to gauge the contribution of anthropogenic stressors to coral reef degradation and to develop and prioritize effective mitigation measures (*e.g.*, policy or technological approaches) for coral conservation. To do this, field work should simultaneously monitor coral health and investigate a variety of environmental conditions (*e.g.*, temperature, pollution, pH, *etc.*) of popular coastal areas and beaches near coral habitats to reflect actual exposure conditions that corals experience.

CRediT authorship contribution statement

M.B.M., P.K.S.L., and T.H. designed the experiment; T.H., M.M.P.T., and A.B.M. carried out the research; T.H., M.M.P.T., and M.B.M. analyzed the data; T.H., M.M.P.T., A.B.M., P.L., T.C., L.W., T.F., P.K.S.L., and M.B.M. wrote the manuscript.

Data availability

Data will be made available on request.

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. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.162744.

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