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Simulating cyanide fishing: photosynthetic effects of short-term cyanide exposure in three different hermatypic coral species

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ABSTRACT

Since the 1960s the demand for ornamental aquarium fish has grown steadily and consequently cyanide fishing is still a popular fishing method despite its prohibition. This poses a severe threat to coral reefs in Southeast Asia. This study aimed to investigate the short-term stress reaction on photosynthetic yield in the tissues of three different hard coral colonies (branching growth forms *Pocillopora damicornis* and *Seriatopora hystrix*, and massive *Porites lobata*) to initially high and then decreasing cyanide exposure, mimicking cyanide fishing by fishermen. Experiments were performed both *in situ* in the coral reefs of the Marine Protected Area Pulau Pieh, West Sumatra, Indonesia, and in the aquaria facilities of ZMT in Germany. A Diving-PAM fluorometer was used for *in vivo* stress assessment of the holobiont. While in all species the photosynthetic efficiency was significantly reduced right after cyanide application, the massive species displayed much lower ΔF/Fm' values. After three days in cyanide-free water all three coral species recovered to initial values of Fv/Fm, except for *P. lobata*. No bleaching or discolouration was detected by the conclusion of the experiment after 38 days. Especially Indonesian reefs with massive corals may be therefore more severely impacted by cyanide fishing since the retention time of the water in these reefs is longer than in reefs that consist primarily of branching corals. This might have implications for the management of different reef parts of the MPA.

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Indonesia; destructive fishing; MPA; photosynthesis; PAM

Introduction

Coral reefs are one of the most valuable and diverse ecosystems, providing home to approximately a third of all marine species (Bowen et al. 2013) and offering numerous ecosystem services ranging from primary production and food supply to tourism and shoreline protection (Sheppard et al. 2018). Coral reefs worldwide are facing serious threats from global factors such as climate change to local anthropogenic activities such as coastal development, over-fishing and destructive fishing methods (Hoegh-Guldberg et al. 2007; Burke et al. 2011). Since the 1960s the demand for ornamental aquarium fish has grown steadily (Barber and Pratt 1998) leading to collections of millions of live reef fish annually (Wabnitz et al. 2003; Rhyne et al. 2017). Unfortunately, the marine aquarium trade uses some of the most destructive fishing methods to coral reefs, which has evoked concerns for several decades (Johannes and Riepen 1995; Barber and Pratt 1998; Herz et al. 2016; Madeira and Calado 2019; Madeira et al. 2020). Ornamental fish are often captured illegally using cyanide, an effective but very destructive fishing method (Johannes and Riepen 1995; Barber and Pratt 1997). The practice is meant to immobilize the fish, but if too much cyanide is applied, both targeted and non-targeted fish can die from overdoses (Cervino et al. 2003).

In addition, cyanide fishing poses a severe threat to many coral reefs in Southeast Asia since it is still a popular fishing method despite its prohibition (Rubec 1988; Barber and Pratt 1998; Rubec et al. 2001). Tablets of sodium cyanide (NaCN) or potassium cyanide (KCN) are diluted in small plastic bottles and then squirted into reef crevices to stun and capture target fish (Halim 2002), but the plume of cyanide is at the same time also affecting corals and other invertebrates. Regarding estimations from the Nature Conservancy for Fisheries in the Komodo National Park in Indonesia, the squirt bottles used by fishermen contained about 1.5–2.0 g l^{-1} of cyanide ($\sim 5 \times 10^{-1}$ M cyanide; Pet and Djohani 1998). Johannes and Riepen (1995) estimated the cyanide concentration in a typical squirt bottle to be up to 10^{-1} M (~4.9 g l^{-1} for NaCN or 6.5 g l^{-1} for KCN, respectively).

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As cyanide effectively blocks the electron transport chain in cell respiration, exposed organisms can die rapidly (Dobbs 2009). As a result of the non-target effects of the fishery practice, corals are exposed to high concentrations of cyanide (10^{-1} M to 10^{-2} M) that can rapidly fall to lower concentrations (10^{-5} M to 10^{-6} M) within seconds to minutes due to hydrological conditions as proposed by Jones and Steven (1997). Previous studies reported that exposing *Pocillopora damicornis* and *Porites lichen* to high NaCN concentrations of 10^{-1} M for 10, 20 and 30 min had led to bleaching (Jones and Steven 1997). Also, shorter exposure (between 2 and 7.5 min) of *P. damicornis* to 10^{-2} M led to bleaching and subsequent death, whereas no algal loss occurred at concentrations below 10^{-3} M (Jones and Steven 1997). In a study from Jones and Hoegh-Guldberg (1999), the explants died at even lower concentrations (10^{-4}–10^{-5} M) when incubated for several hours. Also, coral and giant clam larvae are very sensitive towards cyanide exposure (Werorilangi et al. 2019). This demonstrates that the destructive effect of CN^- ions depends on a combination of concentration and exposure time. Probably also species-specific factors and previous stress levels corals have been exposed to need to be considered.

During a number of dives in coral reefs off West Sumatra the authors had the opportunity to watch the activity of fishermen using destructive fishing practices such as cyanide squirting. As West Sumatra is known for high energy reefs, with mostly strong tidal currents (Kunzmann 1997; Klein and Kunzmann 2001), it can be assumed that exposure times of corals to cyanide are rather short. The above-mentioned previous studies usually exposed coral explants for longer periods of time (except for Jones and Steven 1997, who also included 1, 2.5, 5 and 7.5 -min exposure) and thus do not sufficiently account for rapidly declining cyanide concentrations in reefs owing to the diluting effect of currents. Recently, studies on the effect of cyanide on fish and how this is metabolized into thiocyanate were also published (Herz et al. 2016; Madeira and Calado 2019; Madeira et al. 2020; Murray et al. 2019).

The aim of this study was therefore to simulate cyanide fishing activities and investigate the effect of initially high, but rapidly decreasing cyanide concentrations on the photosynthetic response of the three hard corals *Pocillopora damicornis*, *Seriatopora hystrix* and *Porites lobata* and specifically look into the recovery potential. These coral species usually co-occur in the reefs of West Sumatra and were chosen due to their distinct differences in growth form, growth speed and maximum size. As proxy for the overall coral vitality and fitness, photosynthetic quantum yields (photosynthetic efficiency) were measured to indicate stress effects of the reef-dwelling corals.

Materials and methods

This study consists of two experimental parts, a field and a laboratory experiment. The photosynthetic stress response of the test organisms was determined in both experiments by measuring *in vivo* the chlorophyll *a* fluorescence of photosystem II (PSII), using a portable, submersible pulse amplitude modulated chlorophyll fluorometer (Diving PAM; Walz, Effeltrich, Germany; for details see Schreiber 1986, 2004).

In the field, light-adapted effective PSII quantum yield (ΔF/Fm') of the two coral species *Seriatopora hystrix* (branching growth form) and *Porites lobata* (massive) was measured *in situ*. During laboratory experiments dark-adapted (7–12 min) maximum quantum yield of photosynthesis (Fv/Fm) was determined from the symbiotic dinoflagellates of the hard coral species *S. hystrix* and *P. lobata*, and additionally *Pocillopora damicornis* (branching). These parameters were chosen as indicators of stress-induced damage to PSII and to reflect the current health status of the corals.

A dark adaptation of the coral species in the field could not be performed (except for one short pre-experiment on *S. hystrix* during low current conditions, see Fig. A1 in Appendix), because strong swell and currents prevailed, and the use of black foil for a dark acclimation of the organisms was not possible. However, pre-experiments during low current conditions showed that light- and dark-adapted corals showed little difference in yield values, with those of dark-adapted species being 5.1 ± 0.1% higher after 30 min (Fig. A1).

Field studies

Study site, species investigated and field experiments

Fieldwork was conducted in the reef area of the Marine Protected Area (MPA) Pulau Pieh off Padang, West Sumatra, Indonesia in August 2018 (GPS position −0.874842, 100.100420; for site description and details about the establishment of the MPA in the year 2000 see Kunzmann and Samsuardi 2017, 2018). Initially, ΔF/Fm' of five colonies of the massive coral *Porites lobata* (~0.25 m in diameter) from around 8.0 ± 1.0 m depth and of five colonies of the branching coral *Seriatopora hystrix* (~0.10 m in diameter) from

around 11.0 ± 1.0 m depth was determined. All measurements were conducted at the same day and at the same ambient light levels between 11 am and 2 pm. Using a squirt bottle, 1 litre of a 10^{-2} M potassium cyanide solution (KCN, Sigma-Aldrich, Seelze, Germany) was sprayed onto five coral colonies of the same species (~200 ml KCN each), standing close to each other. After 5 and 30 min of exposure, ΔF/Fm' was measured again at exposed parts of the corals.

Laboratory experiments

All laboratory experiments were conducted in 2019 at the MAREE (Marine Experimental Ecology) aquaria facilities of the Leibniz Center for Tropical Marine Research (ZMT) in Bremen, Germany.

Coral maintenance and propagation

Colonies of the hard corals *Pocillopora damicornis* (green ecomorphs), *Seriatopora hystrix* and *Porites lobata* were kept since 2014 in a 4.0 × 0.9 m-aquaria system (1500 l; artificial seawater SW, Coral Pro Salt, Düsseldorf, Germany) at 26°C (±0.5°C accuracy; temperature sensor Eheim GmbH & Co. KG, Deizisau, Germany), at an absolute salinity (S_A) of 35. Light was provided by LED lamps (Aqua-illumination Hydra 52HD, USA) at an average irradiance of 240 µmol photons m^{-2} s^{-1} of PAR (photosynthetically active radiation) in a 12/12 h diurnal cycle. The aquaria also accommodated clownfish, sea anemones and various other soft and stony coral species. Organisms were fed twice a week with freshly hatched *Artemia salina*.

To gain replicates (sampling units), 2–3 parent coral colonies of each species were fragmented underwater with a pair of pliers or by using an electrical saw to generate 10–12 fragments of about the same size each (fragment sizes from *P. damicornis* and *S. hystrix*: 5–7 cm in length, and from *P. lobata*: about 5 cm in diameter). These fragments were glued to ceramic plugs with coral glue (EcoTech Elements, Allentown, USA) and placed on a grid. They were put back into the aquaria system and given 4 weeks to acclimatize under the same conditions as mentioned before. Before the start of the experiment, photosynthetic efficiency (Fv/Fm initial) of 10 replicate specimens of all three species was measured after a dark adaptation of 7–12 min using a Diving PAM (description of method see above).

Experimental setup

The experiment was performed separately for each of the three species with 10 replicates of fragments. Plugs with coral fragments were placed in a 20 l-experimental glass aquarium filled with 10 l artificial SW (S_A 35), set up in a constant temperature climate chamber at 26°C. Light intensity above the aquaria was set to 250 µmol photons m^{-2} s^{-1} PAR provided by LED lamps (see above). One litre of 10^{-2} M potassium cyanide solution (KCN; Sigma Aldrich, Seelze, Germany) was added to the aquaria by using a squeeze bottle (on top of the corals, simulating fishers) to gain a temporary nominal concentration of 10^{-3} M KCN. After 10 min of light exposure, and followed by 7–12 min of complete darkening of the aquarium, photosynthetic efficiency was measured (Fv/Fm exposure). Thereafter the fragments were transferred to a 20 l-aquarium containing a KCN concentration of 10^{-5} M, simulating a dilution process caused by waves and currents, and Fv/Fm was determined again after 10 min exposure under light (Fv/Fm dilution). The above-mentioned molar concentrations correspond to the following mg l^{-1} concentrations: 10^{-2} M = 650 mg l^{-1}, 10^{-3} M = 65 mg l^{-1} and 10^{-5} M = 0.65 mg l^{-1}.

Finally, coral fragments were moved to a cyanide-free aquarium (same 200 l; 26°C, S_A 35, 250 µmol photons m^{-2} s^{-1}) and the extent of recovery was determined during a recovery period of 3–38 days (Fv/Fm recovery).

In pilot experiments (51 days) no significant differences in Fv/Fm could be discovered between the dilution steps of 10^{-4} M and 10^{-5} M KCN, so that an intermediate dilution to 10^{-4} M KCN was skipped during the main experiments. Furthermore, measurements during the recovery phase were considered completed after 38 days, as there were no significant changes in Fv/Fm detected after that time period. All PAM fluorometric measurements were conducted directly in the experimental tanks at a constant temperature of 26°C.

Statistical analysis

Statistical evaluations (separate one-factor ANOVAs) were carried out using R (Version x64 3.5.1; R Core Team 2017) and the integrated development environment RStudio. The data were tested for normal distribution using Shapiro–Wilk tests and Q-Q-Plots. In order to assess the effects of different concentration levels of KCN onto the photosynthetic efficiency of the three separately tested coral species, generalized linear models (GLM) were used for normal distributed data, and for not-normal distributed data, Kruskal–Wallis tests were performed with the data sets collected in the laboratory. A *P*-value of <0.05 was considered significant (Table I).

Table 1. Summary of the multi-factorial analyses of variance (ANOVA) for the tested variables.

Response variables	Experiment, Figure	Species investigated	Model	Tested value	*P*-value
Light-adapted effective PSII quantum yield (ΔF/Fm')	Field, Fig. 1	*Seriatopora hystrix*	GLM	t0 against t5	<0.001
				t0 against t30	<0.001
				t5 against t30	0.369
		Porites lobata	GLM	t0 against t5	<0.001
				t0 against t30	<0.001
				t5 against t30	0.367
Dark-adapted maximum PSII quantum yield (Fv/Fm)	Laboratory, Fig. 2	*Pocillopora damicornis*	GLM	t0 against 10^{-3}	<0.001
			Kruskal–Wallis	t0 against 10^{-5}	<0.001
			GLM	t0 against rec	0.063
		Seriatopora hystrix	GLM	t0 against 10^{-3}	*<0.001*
			Kruskal–Wallis	t0 against 10^{-5}	*<0.001*
			GLM	t0 against rec	*0.084*
		Porites lobata	GLM	t0 against 10^{-3}	*<0.001*
			Kruskal–Wallis	t0 against 10^{-5}	*<0.001*
			GLM	t0 against rec	*0.589*
ΔF/Fm' versus Fv/Fm	Field, Fig. A1 Appendix	*Seriatopora hystrix*	GLM	t0 against t0	*0.0282*
				t5 against t5	*<0.001*
				t30 against t30	*0.3379*

GLM = Generalized Linear Model, t0 = time 0/initial, t5 and t30 = after 5 and 30 min of exposure to 10^{-2} M KCN, 10^{-3} = exposure to 10^{-3} M KCN, 10^{-5} = dilution to 10^{-5} M KCN, rec = after 3 days of recovery.

Results

Field experiments

A series of preliminary experiments during low current conditions showed that light- and dark-adapted corals exhibited only partially different photosynthetic performances, with dark-adapted species showing slightly higher yield values. Mean values in photosynthetic quantum yield in dark-adapted *Seriatopora hystrix* ($n = 5$) were: Fv/Fm 0.73 ± 0.01(SE) initially, 0.72 ± 0.00 shortly (5 min) after being sprayed with 10^{-2} M KCN, and 0.64 ± 0.04 half an hour after exposure; and light-adapted ΔF/Fm' values were: 0.70 ± 0.01(SE) initially, 0.63 ± 0.01 and 0.61 ± 0.00 five and 30 min after KCN exposure, respectively. In contrast to values of unstressed *S. hystrix*, no significant differences in photosynthetic performance between light- and dark-adapted (7–12 min under black foil) *S. hystrix* colonies were found after 5 and 30 min of exposure to KCN (data are shown in the Appendix, Fig. A1, Table I).

In the field study, branched colonies of *S. hystrix* exhibited an overall higher effective quantum yield of photosystem II (ΔF/Fm') compared with massive *Porites lobata* colonies (0.70 ± 0.01 vs. 0.59 ± 0.03, respectively, Figure 1). However, a short-term exposure to cyanide (a 10^{-2} M KCN concentration was expelled onto the organisms) resulted in a clear decline in ΔF/Fm' in both species directly after application under natural irradiance levels. Here, ΔF/Fm' significantly decreased from an initial value of 0.70 ± 0.00–0.63 ± 0.01; 11% reduction in *S. hystrix* specimens already after 5 min of exposure, while in *P. lobata* photosynthetic efficiency was significantly reduced by 28% (ΔF/Fm' values dropped from 0.60 ± 0.03 to 0.43 ± 0.03, both $P < 0.001$, Table 1). After 30 min of exposure, effective quantum yields of the symbiotic dinoflagellates remained almost unchanged compared with values after 5 min (ΔF/Fm' in *S. hystrix*: 0.61 ± 0.00, and in *P. lobata*: 0.46 ± 0.03).

Laboratory experiments

Fragments of the branching coral species *Pocillopora damicornis* and *Seriatopora hystrix* exhibited an overall higher photosynthetic yield (Fv/Fm initially = 0.64 ± 0.01, and 0.65 ± 0.01, respectively) compared with massive *Porites lobata* (Fv/Fm initially = 0.55 ± 0.01; Figure 2A–C). An exposure to a stable KCN concentration of 10^{-3} M resulted in a significant decrease of Fv/Fm in all three species after 10 min under light (Fv/Fm in *P. damicornis*: 0.49 ± 0.01, *S. hystrix*: 0.57 ± 0.01 and in *P. lobata*: 0.48 ± 0.01; all $P < 0.001$, Table I). Comparably to natural dilution processes in the ocean, a controlled exposure to a diluted 10^{-5} M KCN concentration did also result in a significant change in Fv/Fm after an additional reaction time of 10–15 min ($P < 0.001$), demonstrating that photosynthetic efficiency remained impaired. However, all three coral species showed a high potential for a complete recovery of photosynthesis already after 3 days (*S. hystrix* and *P. damicornis* reached 100% of the initial values), and subsequently Fv/Fm remained stable until the end of the experiment (period of 5 weeks) (Fv/Fm after 38 days in *P. damicornis*: 0.61 ± 0.01, *S. hystrix*: 0.65 ± 0.00 and in *P. lobata*: 0.55 ± 0.01; Figure 2A–C). No bleaching was observed in any of the coral specimens during the 38 days of the experiment.

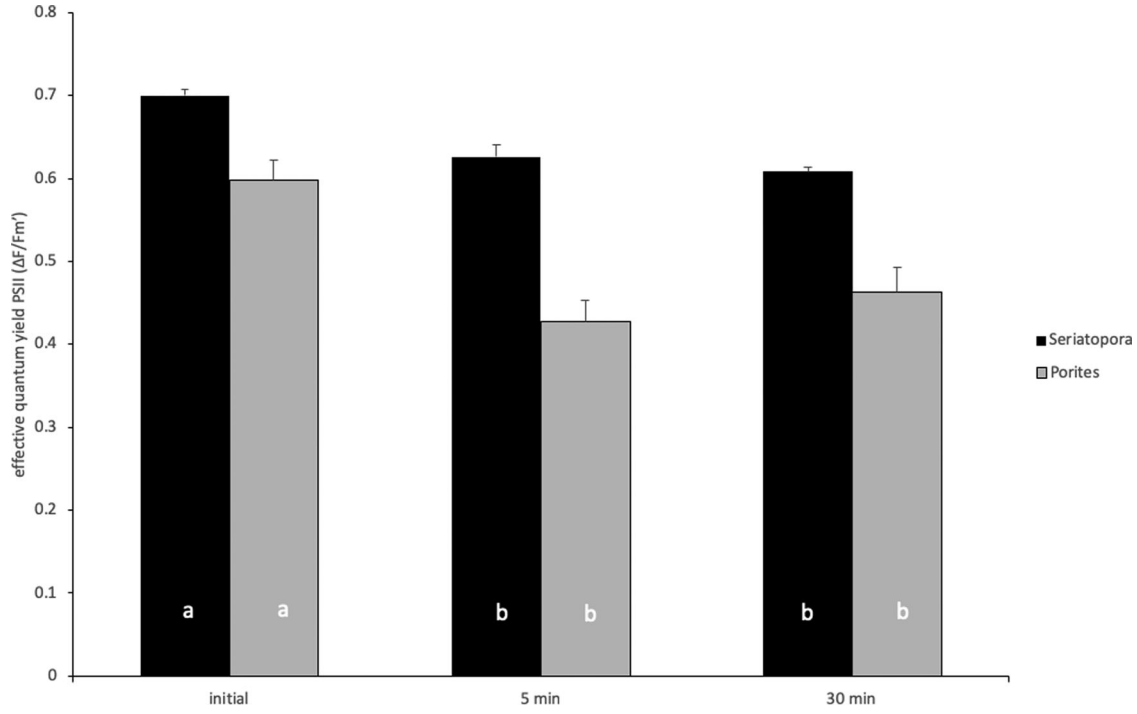

Figure 1. Effective PSII quantum yield (ΔF/Fm') of *Seriatopora hystrix* (black bars) and *Porites lobata* (grey bars) before, right after (5 min) and 30 min after a 10^{-2} M KCN solution was expelled onto the coral surfaces directly in the field (Pulau Air). Different letters indicate significant differences within species treatments (Generalized Linear Model, $P < 0.05$). Data are mean values ±SE ($n = 5$).

Discussion

The aim of the present study was the simulation of cyanide fishing in a coral reef including natural dilution processes of cyanide in seawater. The photosynthetic response of the hard corals *Pocillopora damicornis*, *Seriatopora hystrix* and *Porites lobata* to cyanide exposure was investigated, also taking their recovery potential into account. The three coral species we considered were distinctly different from each other with regard to growth form, growth speed and maximum size, but usually co-occur in reef flats and upper slopes, at least in the coral reefs of West Sumatra. While *P. damicornis* is a branching (thick branches) to submassive species, *S. hystrix* is branching (thin and delicate branches) and *P. lobata* is a massive species. Despite these morphological differences, the responses in photosynthetic efficiency to cyanide exposure are very similar except for the fact that initial values of Fv/Fm for *P. lobata* are slightly lower.

Short exposure of all three investigated coral species to cyanide concentrations of 10^{-2} M (field) and 10^{-3} M (laboratory) caused a significant decrease in photosynthetic quantum yield. This decrease was still visible at reduced cyanide concentrations of 10^{-5} M. Chalker and Taylor (1975) and Barnes (1985) also reported a decrease in photosynthetic activity in *Acropora cervicornis* and *A. formosa* exposed to $>10^{-5}$ M cyanide and Jones and Hoegh-Guldberg (1999) in *Plesiastrea versipora* exposed to 10^{-4} M for 3 hours. Jones and Steven (1997) reported a decrease in respiration for concentrations between 10^{-1}–10^{-3} M in *P. damicornis* and *Porites lichen*.

In contrast to the studies of Jones and Steven (1997), Jones and Hoegh-Guldberg (1999) and Jones et al. (1999), we did not encounter visible bleaching or discolouration in any of the three species used until the end of our experiment (some pre-trials even lasted for 51 days). This is unusual, as bleaching is reported to be one of the first reactions to stressful environmental conditions (Jones and Steven 1997). According to Porter et al. (1989), bleaching results in a loss of photosynthetic potential. In this study the decline in photosynthetic performance occurred without bleaching, suggesting that short-term exposure and rapidly decreasing concentrations of cyanide only affect the immediate photo-biochemical processes. This process seems to be fully reversible, without any long-term (at least 38, or 51 days, respectively) effects. This is true for cyanide concentrations up to 10^{-2}–10^{-3} M, as tested in our study. Future studies should also investigate the immediate and long-term effects of even higher initial concentrations (e.g. 10^{-1} and 1.0 M). In addition, the usually repeated use of

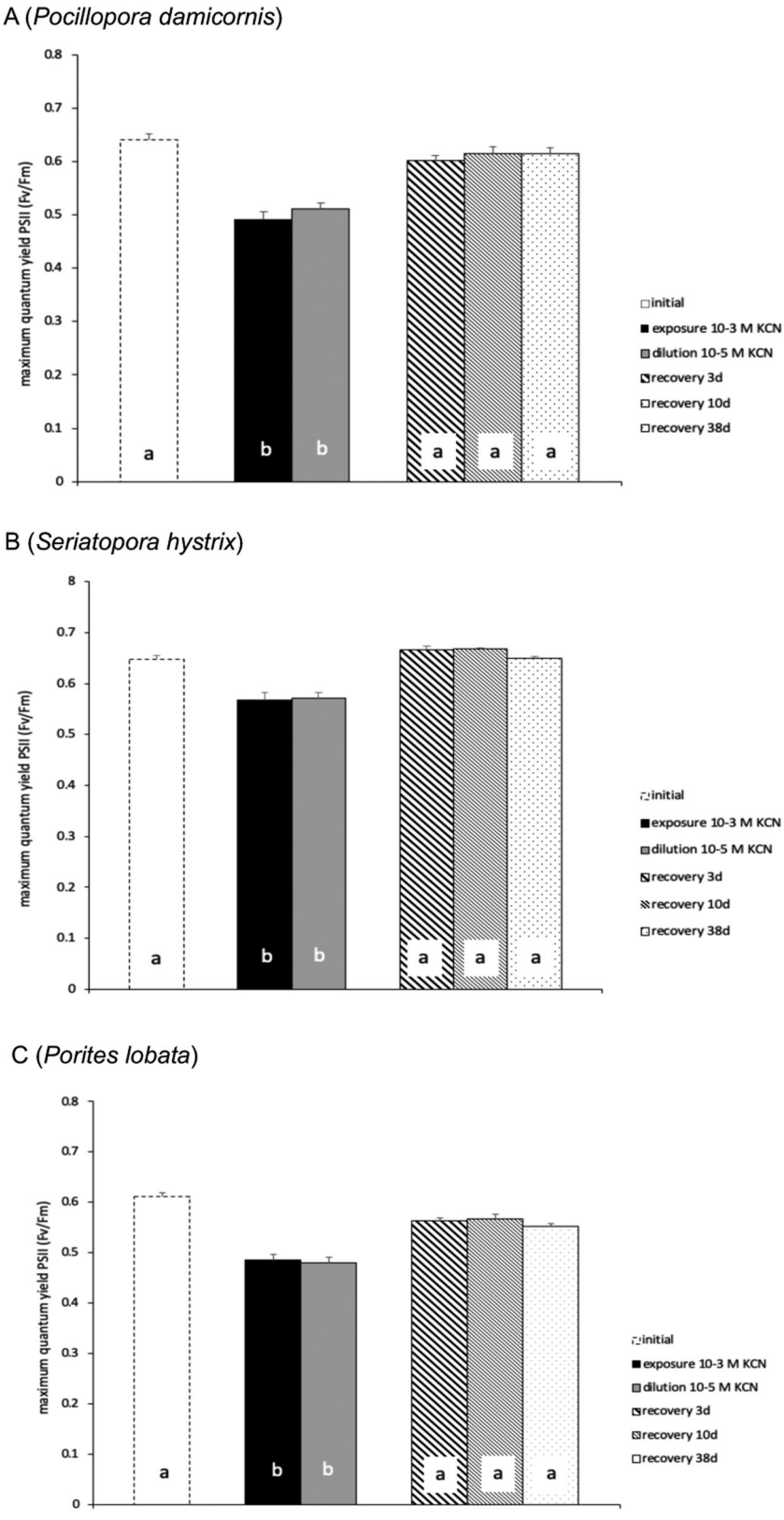

Figure 2. A–C Effect of the exposure to 10^{-3} M KCN, a simulated natural dilution to 10^{-5} M KCN on maximum PSII quantum yield (Fv/Fm) of (A) *Pocillopora damicornis*, (B) *Seriatopora hystrix* and (C) *Porites lobata* and their potentials of photosynthetic recovery over 38 days in an aquarium laboratory experiment. Different letters indicate significant differences between treatments (Generalized Linear Model or Kruskal–Wallis tests, $P < 0.05$). Data represent mean values ±SE ($n = 10$).

cyanide (within weeks or months) by fishermen on the same reef needs to be considered.

However, the corals from this study showed rapid and clear effects of reduced photosynthetic efficiency already after 5 min, which is in good agreement with results from Jones and Steven (1997) (5 and 7.5 min), while Chalker and Taylor (1975) report inhibition of photosynthesis after 30 min and Jones and Hoegh-Guldberg (1999) monitored decreasing photosynthetic values only after 3 days of exposure. A study by Jones et al. (1999) suggests that if a coral is exposed directly to a plume of cyanide, there is an immediate disruption of photosynthetic electron flow in the symbiotic microalgae, possibly through the (inhibiting) effect of cyanide on Calvin cycle enzymes. This explains on one hand the fast reaction time in the present study, and on the other hand also the immediate decrease in respiration in the study by Jones and Hoegh-Guldberg (1999), because of similar inhibition of enzymes in the citric acid cycle.

The three species of the present study also demonstrated a similar and fast recovery potential (within 3 days), with almost identical values for initial and recovering photosynthetic efficiency (Figure 2A–C). Only *P. lobata* showed a slight trend for a not fully completed recovery (but values are not significantly different). Other species (*P. damicornis*, *Porites lichen*) are reported to recover within 7–12 days (Jones and Steven 1997; Jones and Hoegh-Guldberg 1999).

Jones and Steven (1997) reported recovery of respiration rates for *P. damicornis* within 120–140 min after short (2.5–7.5 min) cyanide exposure. After longer exposure (3 h), recovery of Fv/Fm values for *P. versispora* can take 5–6 days, and in the case of higher cyanide concentrations (10^{-3} M) recovery is not completed within 12 days (Jones and Hoegh-Guldberg 1999). The rapid and complete recovery in this study is highly likely attributed to the short exposure time (10–15 min) simulating the dilution effects in high energy reefs. Therefore, cyanide fishing in those environments only affect corals in the immediate vicinity of the cyanide cloud. High wave action also depends on season and moon phases, so locations of high energy reefs can vary. However, a study by Wolanski and Jones (1980) revealed that water can easily get trapped behind large massive corals for up to 30 min. Under such conditions, and also when not squirt bottles, but large 200 litre drums with cyanide are dumped onto reefs, effects are much more drastic causing extensive coral mortality. Especially reefs dominated by massive corals (e.g. the reefs east of the MPA islands Pulau Pieh, Western Sumatra) may therefore be more severely impacted by cyanide fishing since the retention time of the water in these reefs is longer than in reefs that consist primarily of branching corals.

Conclusions

Short-term exposure of corals *P. damicornis*, *S. hystrix* and *P. lobata* to cyanide concentrations of 10^{-3} M caused a significant decrease in photosynthetic efficiency. The decrease in photosynthesis continues at reduced cyanide concentrations of 10^{-5} M. After three days in cyanide-free water all three coral species recovered to initial Fv/Fm values, except for *P. lobata*. No bleaching or discolouration could be observed until 38 days after exposure. Future studies of short-term exposure to cyanide should also look into even higher concentrations of cyanide and into resulting chlorophyll concentrations (potential bleaching) and endosymbiotic dinoflagellates counts (cell densities). This might have implications for the management of different reef parts of the MPA, especially for reefs dominated by massive coral growth forms.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Appendix

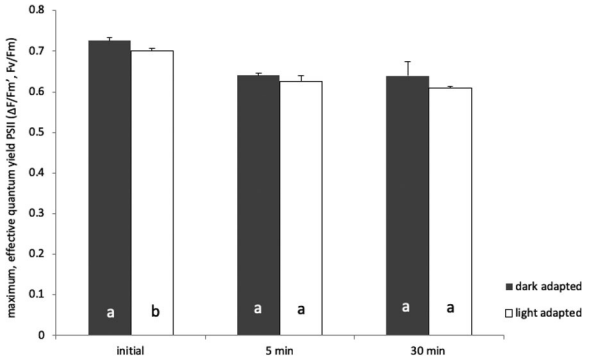

Figure A1. Comparison of dark-adapted maximum PSII quantum yield (Fv/Fm, black bars) and light-adapted effective quantum yield of PSII (ΔF/Fm', white bars) in *Seriatopora hystrix* initially and 5 and 30 min after a 10^{-2} M KCN solution was expelled onto the coral surfaces directly in the field (Pulau Air). Different letters indicate significant differences between treatments (light/dark-adaptation) at each measuring point (Generalized Linear Model, $P < 0.05$). Data are mean values ±SE ($n = 5$).