Effects of transparent exopolymer Particles and muddy terrigenous sediments on the survival of hard coral recruits

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Abstract

Sedimentation is a major cause of mortality in scleractinian coral recruits. In this study, we compared the effects of muddy coastal sediments, with and without enrichment by 'marine snow', on the survivorship of recruits of the hard coral *Acropora willisae*. Transparent exopolymer particles (TEP) were measured as characteristic components of marine snow using a staining method (Passow & Alldredge, Limnol. Oceangr. 40 (1995) 1326). Four-week-old recruits were exposed to: (1) muddy coastal sediments; (2) TEP; (3) TEP-enriched muddy coastal sediments; and (4) unfiltered sea water, for 43 h in aerated flow chambers. Thirty-three percent (± 5 SE) of coral recruits died after 43-h exposure to TEP-enriched muddy coastal sediments ($\sim 14\,\mathrm{mg\,cm^{-2}}$ sediments enriched with $3.8 \pm 0.2\,\mathrm{\mu g\,cm^{-2}}$ gum xanthan equivalents (GX) TEP). In contrast, no or minimal mortality was observed in the other three treatments. Mortality increased to $>80\%$ when the amount of deposited TEP was almost tripled ($10.9 \pm 1.3\,\mathrm{\mu g\,cm^{-2}}$ GX) and sediment increased by 50%. Thus, coral recruits survived short-term exposure to low levels of TEP and low levels of muddy sediments, but sediments enriched with TEP at concentrations recorded at some of the inshore stations proved to be detrimental. Concentrations of TEP were measured in the central Great Barrier Reef (latitude 16–18°S) in summer, the season of coral spawning and recruitment. Within $<10\,\mathrm{km}$ off the coast, TEP concentrations were high (mean $= 291 \pm 49$ SE $\mathrm{\mu g\,GX\,l^{-1}}$, range $= 152$–$791\,\mathrm{\mu g\,GX\,l^{-1}}$). Concentrations declined with increasing distance from the coast, and averaged 83 (± 26 SE) $\mathrm{\mu g\,GX\,l^{-1}}$ around oceanic reefs $>40\,\mathrm{km}$ off the coast. Our study suggests that both sediment composition and short-term (43 h) sediment deposition affect survival of coral juveniles, which has implications for the capacity of inshore reefs to be recolonised by corals to recover from acute disturbance events.

1. Introduction

Sedimentation is a major cause of mortality in the initial life stages of hard corals (Cnidaria: Scleractinia). It can locally reduce recruitment rates (Babcock & Smith, in press; Gilmour, 1999; Sato, 1985), and at higher concentrations affect a range of life history parameters in adult corals (Rogers, 1990). However, with the exception of grain sizes (Fisk, 1981; Stafford-Smith & Ormond, 1992), not much is known about differences in sediment characteristics that may influence the survival of corals exposed to sedimentation. A pilot study indicated that low-level sedimentation of sticky muddy 'marine snow' aggregates affects small reef organisms, such as coral-inhabiting barnacles, more than intermediate amounts of clean sediment (Fabricius & Wolanski, 2000). It is likely that sediment characteristics such as tendencies to form sticky marine snow aggregates, and differences in organic and microbial concentrations, may also alter the effect of sedimentation on coral recruits.

Microbes, diatoms and metazoans such as appendicularians exude dissolved mucopolysaccharides that may become particulate through the formation of cation bridges (Alldredge, Cole, & Caron, 1986; Hansen,

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Kiørboe, & Alldredge, 1996; Logan, Passow, Alldredge, Grossart, & Simon, 1995). Such particles are known as transparent exopolymer particles (TEP) (Passow & Alldredge, 1994). Microbes and diatoms that bloom in the water column, or colonise suspended and sedimented particles, can promote the formation of TEP by releasing dissolved polysaccharides (Ayukai & Wolanski, 1997; Kiørboe, Andersen, & Dam, 1990; Passow, Alldredge, & Logan, 1994, Wolanski, Spagnol, & Lim, 1997, detailed information to the formation of TEP was reviewed by Passow, 2000). At moderate turbulence, TEP collide with other suspended particulate matter, and their stickiness facilitates the development of composite marine snow aggregates that can grow to sizes >500 µm Fig. 1; Eisma, 1986; Passow & Alldredge, 1994; Wolanski & Gibbs, 1995). During calm periods the aggregates settle out from the water column and are deposited on benthic organisms and the surrounding sea floor (Wolanski, Spagnol, & Ayukai, 1998). Thus TEP plays an important role in the formation of macroaggregates and in sedimentation processes (Logan et al., 1995). They also serve as substrate for microbes and as particulate food for grazers (Alldredge et al., 1986).
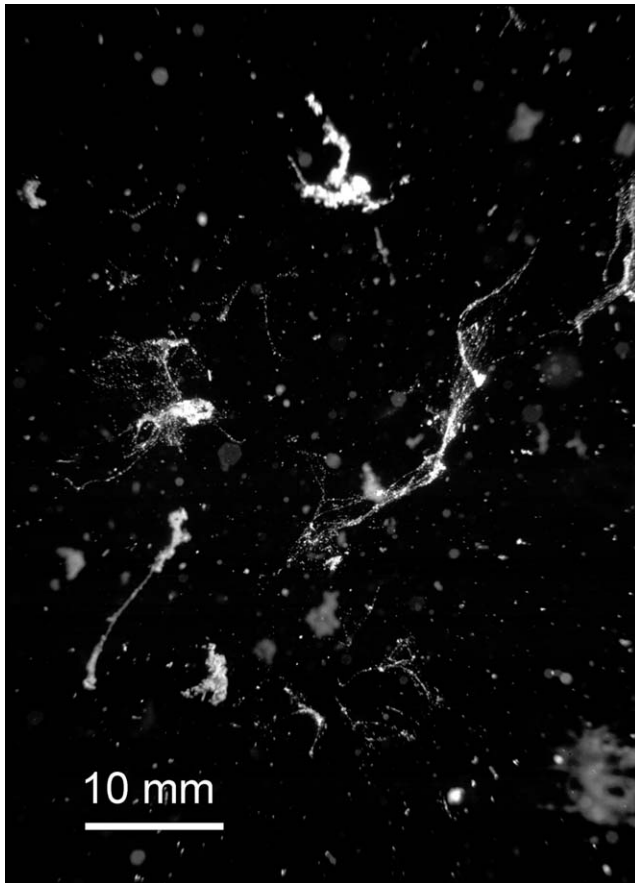

Fig. 1. Suspended sediment colliding with large TEP to form 'marine snow' aggregates.

Riverine flood plumes originating from wet tropical agricultural lands in Queensland (East Australia, latitude 16–18°S) discharge high concentrations of dissolved and particulate nutrients and sediments into the Great Barrier Reef (Devlin, Waterhouse, Taylor, & Brodie, 2001; Wolanski, 1994). Such flood plumes are the largest external source of nutrients for the GBR lagoon (Furnas & Mitchell, 2001; Furnas, Mitchell, & Skuza, 1997). Although a link between nutrient availability and TEP formation has not been established, it is conceivable that nutrients injected by riverine flood waters may promote the growth of TEP-producing diatoms and bacteria. Periods of high concentrations of TEP can coincide with high concentrations of suspended particulate matter—either newly imported with the flood plume, or re-suspended from the shallow sea floor. In inshore areas of the Great Barrier Reef, such co-occurrences are particularly likely during monsoonal summer rain. Early summer (November to December) is also the time of mass spawning of many reef invertebrates including the reef-building hard corals. A few days or weeks after the mass spawning event, coral larvae settle on suitable substratum. They metamorphose to primary polyps, which soon start depositing their calcium carbonate skeleton, and add new polyps by budding. After 4–6 weeks, these recruits measure up to 2 mm in diameter and 1 mm in height, and consist of one to six polyps (K. Fabricius, personal observation). This early post-settlement time is likely to be the most vulnerable stage in the benthic life phase of a coral. The ability of young coral recruits to survive local exposure to sedimentation or other adverse environmental conditions has large-scale consequences for the capacity of coral reef communities to recover from disturbance events.

In this study, we tested the short-term effects of deposition of TEP-enriched muddy marine snow and sediments on the survival of recruits of hard corals (Cnidaria: Scleractinia), by exposing them to sediments with and without TEP-enrichment. We also present data on summer concentrations of TEP in the central Great Barrier Reef off the wet tropical agricultural lands in Queensland, in order to determine what levels of TEP are likely to be encountered by coral recruits in inshore waters of the central Great Barrier Reef.

2. Materials and methods

2.1. Experimental study of the survival of coral recruits

The effects of TEP, muddy sediment, and a combination of both, on the survival of 4–6-weeks-old coral recruits was determined experimentally. Recruits were obtained following the protocol of Heyward and Negri (1999): The egg–sperm bundles from 10 colonies of

Acropora willisae (collected from an inshore reef off Townsville a few days before the predicted mass spawning), were mixed for cross-fertilisation, and distributed over 12 10-l buckets in a water bath. Gentle aeration and water flow-through was applied 12 h later to each bucket (plankton mesh was glued over the outflow). After 2 days, 96 unglazed $5.5 \times 5.5 \, cm^2$ terracotta tiles, pre-conditioned by immersion in the coastal sea for 3 weeks, were added to the buckets as settlement substrata, and the larvae settled and metamorphosed on the recruitment tiles 3–5 days later. Eight days after the spawning, the recruitment tiles were vertically suspended on ropes in a $3 \, m^3$ flow-through outdoor tank under 70% shade cloth, in which a circular current of about $3 \, cm \, s^{-1}$ was created by pumps. When the recruits were 26 days old, the experiments commenced. Eight tiles were randomly selected of the 40 tiles with the highest density of recruits. The position, number of polyps, and state (alive, i.e. healthy tissue visible; and dead, i.e. bare skeleton without tissue) of each recruit was mapped on the upper side of each tile using a dissecting microscope. The number of live recruits per upper tile surface averaged 9.75 ± 6.9 (SD) at the beginning of the experiment.

Fine, muddy subtidal sediment was collected from behind a breakwater protecting the mouth of a small creek off Magnetic Island. Coarse material was removed with a set of sieves, and the $<125 \, \mu m$ sediment fraction was kept in aerated sea water until further use. Water rich in TEP was collected from the outflow of a $\sim5000 \, l$ prawn holding tank at the AIMS mariculture facility. Flow-through was stopped overnight after the prawns were fed in the afternoon. The next morning, water from the mid-water column of the prawn tank was collected in a 150-l container. Water samples were taken to analyse TEP, nutrient, and chlorophyll contents: these were similar to those of natural inshore seawater, except for elevated nitrogen and phosphorus concentrations in the prawn tank water (Table 2). Aggregates were allowed to settle for 30 min, then most of the nutrient-rich surface water was siphoned off and discarded, and 10 l from the bottom of the container were used for the experiment.

Four treatments were established (Sediment, TEP, Sediment and TEP, and unfiltered sea water without particle addition as Control) as follows. Four 12-l flow chambers were set up in a controlled temperature room

at $26 \, ^{\circ}C$ (9.5 h light/14.5 h dark) and filled with un-filtered sea water. The TEP-enriched water was mixed, subdivided into two equal lots, and each lot was added to two of the flow chambers containing 7 l of unfiltered sea water. Fifty ml of the wet sediment was suspended in 1 l of seawater, stirred vigorously, and divided into two aliquots. One aliquot was added to a chamber with only unfiltered seawater (Sediment), the other to a chamber containing TEP-enriched seawater (Sediment and TEP). Neither sediment nor TEP was added to the fourth tank (Control). Propellers provided gentle unidirectional flow of $2 \, cm \, s^{-1}$ (imitating conditions on back reef slopes at calm days), and an aquarium air pump was used to aerate the chamber water through air stones. Two tiles were placed horizontally, with the mapped recruits on the upper side, in each chamber. Duplicate water samples from each flow chamber were analysed for TEP concentrations at the beginning of each run (Table 1). The recruits were exposed to the treatments for 43 h; most of the particulate material settled on the chamber floor and on the tiles within $<4 \, h$.

After 43 h, the tiles were carefully removed from the flow chambers, and deposited material was rinsed off each tile with filtered seawater into separate jars. All previously mapped coral recruits were again allocated to the categories alive and dead. The water from the jars was mixed vigorously and subdivided into four sub-samples, which were filtered at low vacuum (15 mg kPa) onto polycarbonate membrane filters (47 mm diameter) with nominal pore size of $0.4 \, \mu m$. Two of the subsamples were dried and weighed to determine the weight of particulate matter deposited per unit area of tile surface (Table 1), the other two subsamples were used for TEP determination, as described below.

The recruits survival experiment was run five times, each time using eight new tiles, TEP newly obtained from the prawn tank, and a new subsample of the sediment batch. Each time the allocation of treatments to the four flow chambers was systematically varied.

Logistic regression, which is able to deal with proportional data and binomially distributed error terms (Collett, 1991), was used to assess the dependence of survival of the coral recruits on the four treatments (TEP, Sediment, Sediment and TEP, Control). In Run 3, TEP concentration was increased 3-fold and sediment

Table 1
TEP concentration suspended in the water of the flow chambers at the beginning of the runs, and amount of TEP and sediments deposited on the recruitment tiles at the end of the runs (eight tiles per run, two tiles per treatment)

Treatment	TEP suspended ($\mu g \, GX \, l^{-1}$)		TEP deposited ($\mu g \, GX \, cm^{-2}$)		Sediment deposited ($mg \, cm^{-2}$)	
	Runs 1, 2, 4, 5	Run 3	Runs 1, 2, 4, 5	Run 3	Runs 1, 2, 4, 5	Run 3
Sediment	292 ± 143	429	2.40 ± 0.40	6.62 ± 3.09	13.8 ± 3.42	14.4 ± 3.06
TEP	566 ± 119	1626	4.67 ± 0.30	13.9 ± 2.64	3.95 ± 0.73	9.27 ± 1.50
Sediment and TEP	465 ± 80	1201	3.83 ± 0.15	10.9 ± 1.28	13.7 ± 3.51	20.3 ± 1.73
Control	76 ± 44	48	0.65 ± 0.15	2.03 ± 0.25	1.04 ± 0.23	2.21 ± 0.31

Table 2
Summary water column properties of inshore, midshelf, and outer shelf reefs of the central Great Barrier Reef during Voyage 1 (December 1999) and Voyage 2 (January 2000), and from the outflow of the prawn tanks, as used in the experiments

Source	N	Distance to coast (km)	TEP (µg GX l⁻¹)	Salinity (PSU)	SS (mg l⁻¹)	Chl (µg l⁻¹)	Phae (µg l⁻¹)	PN (µmol l⁻¹)	TN (µmol l⁻¹)	PP (µmol l⁻¹)	TP (µmol l⁻¹)
Voyage 1											
Inshore	9	1.4 ± 0.3	176 ± 23	34.5 ± 0.1	3.22 ± 0.46	0.49 ± 0.04	0.22 ± 0.02	2.62 ± 0.31	8.44 ± 0.56	0.109 ± 0.008	0.19 ± 0.001
Midshelf	6	18 ± 2	139 ± 60	35.0 ± 0.1	2.27 ± 0.53	0.35 ± 0.03	0.16 ± 0.02	2.41 ± 0.29	8.25 ± 0.66	0.079 ± 0.008	0.18 ± 0.02
Outer shelf	4	45 ± 3	83 ± 26	35.1 ± 0.01	1.67 ± 0.21	0.26 ± 0.04	0.12 ± 0.02	2.02 ± 0.16	6.35 ± 0.39	0.066 ± 0.008	0.13 ± 0.01
Voyage 2											
Inshore	15	1.6 ± 0.2	388 ± 46	34.0 ± 0.1	1.90 ± 0.16	0.40 ± 0.06	0.20 ± 0.03	1.83 ± 0.20	11.71 ± 0.79	0.078 ± 0.007	0.14 ± 0.01
Midshelf	3	15 ± 0.3	205 ± 42	34.4 ± 0.2	1.68 ± 0.55	0.21 ± 0.09	0.11 ± 0.04	2.14 ± 0.63	9.96 ± 0.05	0.045 ± 0.003	0.09 ± 0.01
Mean inshore	24	1.5 ± 0.2	308 ± 37	34.2 ± 0.1	2.40 ± 0.24	0.44 ± 0.04	0.21 ± 0.02	2.06 ± 0.19	10.45 ± 0.61	0.095 ± 0.01	0.16 ± 0.01
Prawn tank	4	N/A	320 ± 15	30.8 ± 0.03	3.42 ± 0.16	0.50 ± 0.02	0.33 ± 0.03	6.58 ± 1.98	24.18 ± 0.36	1.15 ± 0.21	2.06 ± 0.05

The data represent untransformed means ± SE. N, number of samples; SS, suspended solids; Chl, chlorophyll; Phae, phaeopigments; PN, particulate nitrogen; TN, total nitrogen; PP, particulate phosphorus; TP, total phosphorus.

increased 1.5-fold (Table 1); this run was treated separately in the analyses. All statistical analyses used S-Plus Version 2000 (Statistical Sciences, 1999).

2.2. Water sampling and analytical methods

Water samples were collected on the shallow continental shelf of the Great Barrier Reef between 16 and 18°S latitude on two field trips, to determine in situ levels of TEP. During Voyage 1 (December 1999), stations were positioned both along the shore in the inshore region (nine samples from five stations <10 km off the coast) and across the shelf (six samples from three midshelf stations 10–25 km off the coast, and four samples from two outer shelf stations ≥40 km off the coast, Table 2). At each station of Voyage 1, a sample was collected from 5 m depth with a 20-l Niskin bottle lowered from the deck of the research vessel while the ship was anchored ∼200 m behind a reef. A second water sample was collected by a snorkeler, bringing three lots of water from 5 m depth and 1 m above the coral reef in a 5-l Niskin bottle to the surface, where the three Niskin bottle contents were combined in a rinsed bucket. Two reefs were visited twice, with a 5-day interval between the visits (Double Island and Alexandra Reef, Table 3). The results, as expected, identified the inshore area as region of highest TEP concentrations. During Voyage 2 (January 2000), the sampling therefore focused predominantly on inshore waters. At each of the 18 stations of Voyage 2, one sample was collected from 5 m depth with the 20-l Niskin bottle lowered from the deck of the vessel. During this Voyage, 11 of 18 stations were located away from coral reefs, and Double Island was again visited twice.

The water samples were subsampled as follows. For the determination of dissolved silicate, ammonium, nitrite, nitrate, and phosphate, 10 subsamples (10 ml each) were filtered through 0.45 µm Sartorius Minisart Cellulose acetate filters, and frozen at −20 °C. For the determination of salinity, a 500 ml subsample was stored in a tightly closed bottle at room temperature. For the determination of chlorophyll *a*, particulate nitrogen, and phosphorus, six subsamples (100–250 ml) were filtered onto pre-combusted 0.2 µm Whatman GF/F 25 mm filters, and frozen at −20 °C. For the determination of suspended solids, duplicate subsamples (500 or 1000 ml) were filtered onto pre-weighed polycarbonate filters of 0.4 µm pore width, which were later dried at 80 °C for 24 h, and re-weighed. All samples were later processed at the Australian Institute of Marine Science using standard procedures (described in detail in Furnas & Mitchell, 1996).

To determine TEP concentrations, generally two to four (Table 3) subsamples of the seawater (100–1000 ml, depending on the observed aggregate density) were filled into separate jars, preserved with formalin (final

Table 3
Mean TEP concentrations, and number of subsamples analysed (N)

Station number	Date	Reef	Distance to coast (km)	N	TEP concentration ($\mu g\,GX\,l^{-1} \pm SE$) (Ship)	N	TEP concentration ($\mu g\,GX\,l^{-1} \pm SE$) (Reef)
1	14.12.1999	Double Island	1	2	334 ± 33	2	564 ± 23
2	15.12.1999	Alexandra Reef	1	2	531 ± 14		
3		Low Island	15	2	201 ± 18	1	276
4	16.12.1999	Snapper Island	3	2	125 ± 67	1	185
5		Cape Tribulation	1	2	210 ± 53	2	94 ± 67
6	17.12.1999	Norman Reef	50	2	45 ± 3	1	157
7		Hastings Reef	40	2	80 ± 20	2	51 ± 8
8	18.12.1999	Upolu Reef	25	2	130 ± 59	2	44 ± 37
9		Alexandra Reef	1	2	180 ± 42	2	132 ± 42
10	19.12.1999	Double Island	1	2	158 ± 37	2	162 ± 49
11		Green Island	15	2	23 ± 1	2	29 ± 3
12	4.1.2000	Dunk Island	3	2	247 ± 83		
13		Mourilyan Inlet	<1	3	791 ± 58		
14		Russell River	<1	4	300 ± 27		
15		Fitzroy Island	12	5	270 ± 55		
16	5.1.2000	Trinity Inlet	<1	4	339 ± 37		
17		Double Island	1	4	279 ± 44		
18		Garioch Reef	2	3	445 ± 132		
19		Port Douglas	<1	4	374 ± 81		
20		Daintree River	<1	3	377 ± 64		
21		Cape Tribulation	2	2	748 ± 50		
22		Snapper Island	3	3	430 ± 27		
23		Daintree River	2	3	193 ± 29		
24		Low Island	15	3	222 ± 29		
25	6.1.2000	Double Island	3	3	498 ± 14		
26		Yorkey's Knob	1	7	337 ± 37		
27		Cairns Fairleader	1	4	252 ± 52		
28		Mission Bay	1	2	197 ± 48		
29		Green Island	15	4	125 ± 26		

In Voyage 1 (Stations 1–11), samples marked with 'Ship' were taken 200 m away from coral reefs, samples marked with 'Reef' were taken 1 m above coral reefs. In Voyage 2 (Stations 12–29), all samples were taken from the ship. Stations <10 km off the coast are classified as inshore, 10–25 km are midshelf, and ≥40 km are outer shelf.

concentration: 2%), and stored at 4 °C. For further analyses, the subsamples were filtered at low vacuum (15 kPa) onto polycarbonate membrane filters (47 mm diameter) with 0.4 μm nominal pore size, and the filters transferred to a Petri dish. Concentrations of TEP were determined following Passow and Alldredge (1995). The material on the filters was stained for 2–5 s with 500 μl of a freshly filtered (0.2 μm) 0.02% aqueous solution of Alcian Blue (8 GX, ICN Biomedicals, Aurora, USA) in 0.06% acetic acid (pH 2.5). They were then gently rinsed twice with distilled water to remove excessive dye, and transferred to 30 ml beakers containing 6 ml of 80% sulphuric acid. After 2 h extraction, during which the beakers were gently shaken four to six times, the concentration of pigment in the sulphuric acid was spectrophotometrically determined at 787 nm. A calibration factor for each newly mixed staining solution was established following Passow and Alldredge (1995), using gum xanthan (practical grade, ICN Biomedicals) as standard. Based on these calibrations, TEP concentrations are presented as gum xanthan equivalents per liter ($GX\,l^{-1}$).

Linear regression models were used to test for relationships between concentrations of TEP and sediment, chlorophyll, or nutrients. The concentration of TEP (double-square-root transformed) was the response variable, and sediment, chlorophyll, or nutrients, and voyage number, were used as explanatory variables.

3. Results

3.1. Survival of coral recruits exposed to TEP and muddy sediment

In the four experimental runs with low TEP and sediment exposure (Table 1), the mortality in coral recruits differed among the four treatments ($\chi^2_{(3)} = 55.2$, $P < 0.0001$, Fig. 2a). Mortality in the Sediment and TEP treatment (TEP: $570\,\mu g\,GX\,l^{-1}$ suspended ($3.8\,\mu g\,GX\,cm^{-2}$ deposited), sediment: $14\,mg\,cm^{-2}$) averaged 33.2%. No recruits died in the Control or the Sediment treatment, and only one from a total of 74 recruits (3.3%) died in the TEP treatment. The Sediment and TEP treatment thus contrasted strongly to the remaining treatments ($\chi^2_{(1)} = 53.65$, $P < 0.0001$), but there were no differences among the latter three ($\chi^2_{(2)} = 1.55$, $P = 0.461$).
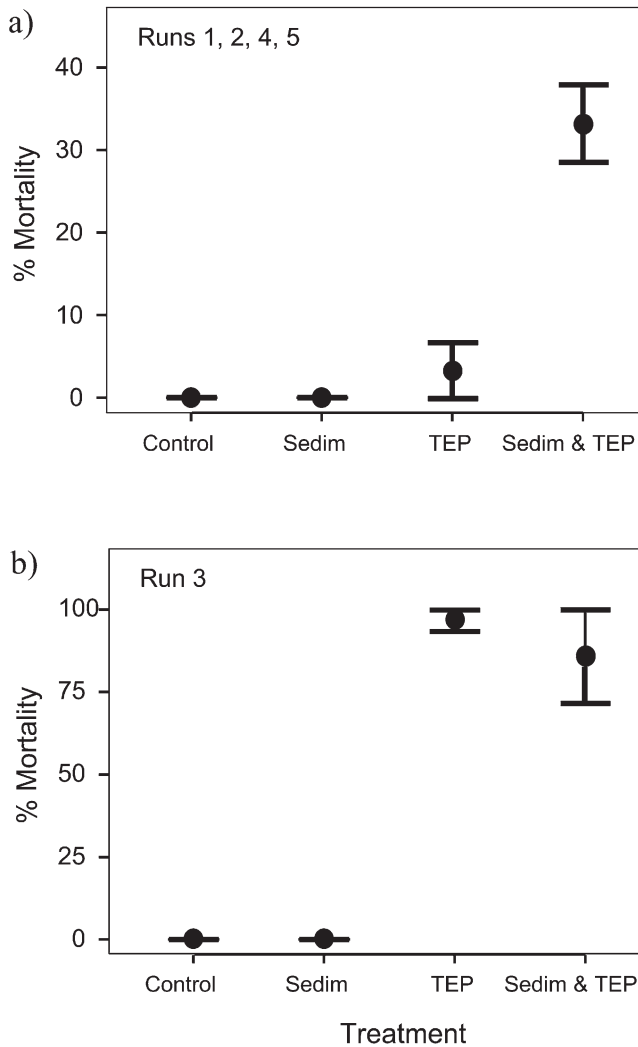
Fig. 2. (a,b) Percent mortality of young recruits of the coral *A. willisae* exposed to a 43-h deposition of muddy coastal sediment ('Sedim'), TEP-aggregates ('TEP'), TEP adhering to muddy sediment ('Sedim and TEP'), and unfiltered seawater without particle addition ('Control'). Data are mean mortality per run and treatment, ±1 SE. Each run included eight tiles carrying live recruits (two per treatment). Concentrations of sediment and TEP applied in the experiments are listed in Table 1.

In Run 3, the TEP load was tripled and sediment increased by ∼50% (TEP: 1200 µg GX l^{-1} suspended (11 µg GX cm^{-2} deposited), Sediment: 20 mg cm^{-2}; Table 1) resulted in mortality rates of 81.8% in the Sediment and TEP treatment, 98.4% in the TEP treatment, and 3.8% in the Sediment treatment (Fig. 2b). None of the recruits died in the Controls.

3.2. TEP concentrations in the field

During Voyage 1, highest values of TEP, suspended solids, chlorophyll *a*, phaeopigments, and particulate phosphorus occurred on the inshore reefs (<10 km from the coast). Concentrations decreased towards the midshelf, and were lowest on the outer shelf reefs (>40 km offshore, Tables 2 and 3). TEP concentrations averaged 176 µg GX l^{-1} (range = 94–531) on inshore reefs, 139 µg GX l^{-1} (range = 24–276) on the midshelf, and 83 µg GX l^{-1} (range = 45–157) on the outer shelf. Concentrations of suspended solids and chlorophyll were also about twice as high inshore compared with outer shelf waters, and salinity increased from 34.47 ± 0.11 PSU (±SE) inshore to 35.12 ± 0.005 PSU around the outer shelf reefs (Table 2). Particulate and total nitrogen showed only weak cross-shelf patterns, possibly because of the presence of some nitrogen-fixing *Trichodesmium*. There was no difference between samples taken 1 m above the reef, to those taken from the ship about 200 m away from the reef (paired *t*-test: $t_{(9)} = -0.642$, $P = 0.537$).

On the second, mostly inshore voyage, no long-shore pattern was found in TEP (Table 3). TEP concentrations in the inshore samples averaged 388 ± 46 µg GX l^{-1}. They were particularly high in several coastal areas, with the highest concentration of 791 ± 101 µg GX l^{-1} recorded in Mourilyan River estuary south of Cairns. The lowest mean value of Voyage 2 was recorded off the Daintree River (Station 23: 193 ± 51 µg GX l^{-1}). Concentrations of TEP, chlorophyll *a*, phaeopigments, and phosphorus again tended to be higher, and salinity was lower, in the 15 inshore samples compared to the three midshelf samples (Table 2).

Concentrations of TEP increased with concentrations of suspended solids in the water (data from both voyages combined: $t_{(34)} = 4.41$, $P = 0.0001$, Fig. 3); the rate of increase being independent of voyage ($t_{(33)} = -0.59$, $P = 0.560$). TEP concentrations were higher during Voyage 2 than Voyage 1 ($t_{(34)} = 7.42$, $P < 0.0001$) for a given concentration of suspended solids. In contrast,
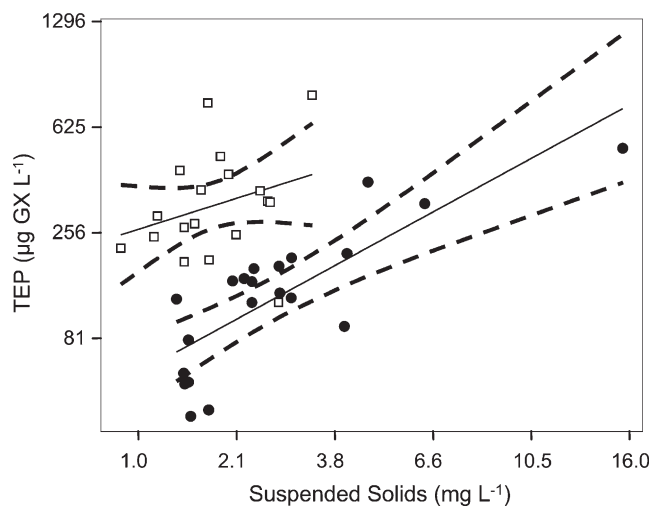

Fig. 3. Relationships between concentrations of TEP (in µg GX l^{-1}), and suspended solids (mg l^{-1}) in the Cairns area. Black filled circles indicate samples from Voyage 1, open squares are from Voyage 2. Values are backtransformed from double-square root transformation for ease of interpretation. Dashed lines indicate 90% confidence limits.

concentrations of TEP were independent of concentrations of chlorophyll, phaeopigments, particulate nitrogen, particulate phosphorus, salinity, and all of the dissolved nutrients during both field trips ($P > 0.05$). TEP concentrations varied greatly between samples and days (e.g. Double Island that was visited four times: (mean $= 333\,\mu g\,GX\,l^{-1}$, range $= 158–564\,\mu g\,GX\,l^{-1}$).

4. Discussion

Our study demonstrated that sediments rich in TEP can damage recruits of the inshore coral *A. willisae* within less than 2 days of deposition, well within the time frames of natural sediment deposition events. Mortality of *A. willisae* recruits was 0% below $400\,\mu g$ $GX\,l^{-1}$ TEP concentration, and high when TEP concentrations exceeded $1000\,\mu g\,GX\,l^{-1}$ ($\sim 10\,\mu g\,GX\,cm^{-2}$ after deposition). The mechanisms of damage are still unknown, however, anoxia under the sediment, and toxic metabolites of microbes associated with the TEP aggregates may contribute to produce synergistic damaging effects. In the northern Adriatic Sea, large marine snow aggregates have been shown to contain various types of toxins, some of which inhibit the P-glycoprotein (Pgp) extrusion pump responsible for mediating the outward transport of toxins in aquatic organisms (Müller et al., 1998). Mass killings of benthic organisms exposed to marine snow in the Adriatic Sea have been linked to the presence of these toxins (Müller et al., 1998), and to anoxia (Herndl, 1988; Stachowitsch, 1984).

Tolerance to sediment exposure varies widely among coral species, but experimental sediment application of $200–800\,mg\,cm^{-2}$ to adult corals have commonly reported physiologically impaired performance or death of underlying tissue (reviewed in Philipp & Fabricius, 2003; Rogers, 1990; Stafford-Smith, 1993). Our present study indicates that recruits of *A. willisae* were able to survive sedimentation levels of $<14\,mg\,cm^{-2}$ for 43 h if the sediment contained little TEP, whereas the same amount of sediment induced mortality within 43 h when it was enriched with TEP. A relatively low sediment tolerance in coral recruits has been previously documented: for example, clay sediment deposition rates of $2–12\,mg\,cm^{-2}\,day^{-1}$ reduced the number of larvae of *Acropora millepora* settling and surviving for 8 months in the field (Babcock & Smith, in press), and sedimentation rates of $3–7\,mg\,cm^{-2}\,day^{-1}$ decreased the number of larvae of *A. millepora* settling on upper surfaces of tiles in tanks (Babcock & Davies, 1991). Thus evidence is increasing that the threshold level for young coral recruits to survive sedimentation is up to two orders of magnitude lower than that of adult corals.

A survival threshold value of TEP (i.e. a concentration below which no mortality occurs in a given period of exposure time) is not easily identified. It needs to incorporate sedimentation levels, as TEP and sediments affected the corals in a synergistic fashion, and both variables were strongly correlated in the field. The estimate of a threshold value is further compromised by the fact that TEP concentrations appear to be systematically underestimated in the presence of sediments. This artefact may be caused by a blockage of actively binding molecular groups by mud aggregates, preventing Alcian Blue to bind to the TEP molecules (U. Passow, personal communication). This may also explain why in this study, TEP concentrations appeared to be consistently lower in the Sediment and TEP treatment than those in the TEP treatment. In addition, comparisons of experimental and field data to derive a threshold value must account for differences in the depths of the water columns in flow chambers and reef (0.15 m and up to 10 m, respectively): if we simplistically assume that TEP deposition per unit substratum area underneath a water column is proportional to the length of the water column, it becomes obvious that rates of aggregate deposition on reefs may be manyfold greater than those simulated in the laboratory.

Nitrogen and phosphorus concentrations in the TEP treatment were higher than those in the other treatments, even after dilution of the water from the prawn tank with unfiltered sea water. Elevated nutrient levels are known to alter the photophysiology and calcification rates of adult scleractinian corals, but do not tend to directly kill corals (Marubini & Davies, 1996; Muscatine, Falkowski, Dubinsky, Cook, & McCloskey, 1989). The 97% survival of recruits in the 'TEP only' treatment in the experimental runs 1, 2, 4, and 5 indicates that the nutrients in the prawn farm water were not responsible for the observed mortality in the TEP and Sediment treatment, and the TEP treatment in Run 3.

To our knowledge, TEP has not been quantified in tropical marine systems prior to this study. TEP concentrations exceeded $400\,\mu g\,GX\,l^{-1}$ at several inshore stations during our surveys (Table 3: Mourilyan Inlet, Double Island, Alexandra Reef, Garioch Reef, and Cape Tribulation Reef). In contrast, TEP values remained well below $400\,\mu g\,GX\,l^{-1}$ at all mid- and outer shelf stations (maximum: $276\,\mu g\,GX\,l^{-1}$). Concentrations in inshore waters of the central Great Barrier Reef in summer (mean $= 291$, range $= 152–791\,\mu g\,GX\,l^{-1}$) were on the higher end of the range of those recorded from shallow inshore areas in other (temperate climate) regions. For example, TEP values in the Monterey Bay of California ranged between 50 and $310\,\mu g\,GX\,l^{-1}$ in summer (Passow & Alldredge, 1995), and in the Kieler Bucht of the Western Baltic Sea between 50 and $200\,\mu g\,GX\,l^{-1}$ (Kraus, 1997), whereas other parts of the Baltic Sea contained $241\,\mu g\,GX\,l^{-1} \pm 66$ SE (Engel & Passow, in press). Our TEP concentrations in the oceanic

waters around the outer shelf reefs (mean = 83, range = 29–157 μg GX l^{-1}) were, however, comparable to those recorded from the open Atlantic Ocean near Bermuda (mean = 53, range = 27–294 μg GX l^{-1} s^{-1}; Engel, Koeve, & Zeitzschel, 1997), despite the fact that our samples were collected near coral reefs. The values were also similar to those recorded from the reef flat of Heron Islands, a midshelf reef in the Southern Great Barrier Reef, where TEP concentrations averaged 44 μg GX l^{-1} (range = 29–73 μg GX l^{-1}; C. Wild, unpublished data).

Patterns of TEP distribution and causes of TEP production (and removal or decomposition) are likely to be complex and multi-causal around tropical coral reefs, and more measurements are needed to adequately determine spatial and temporal patterns and the origin of TEP in the region. Extensive microscopy of live, unpreserved subsamples from each station of Voyage 1 revealed that marine snow aggregates were predominantly composed of mixed amorphic and decomposed detrital material complemented by transparent particles, and a diverse array of fecal pellets, diatom cells and chains, and ciliates (Wild, 2000). There was no difference between TEP concentrations in samples taken by divers just 1 m above corals compared to those taken 200 m away from reefs, instead TEP concentrations above and around coral reefs strongly decreased with increasing distance from the coast. These data suggest that TEP values were probably little affected by the mucus production of scleractinian corals, octocorals and other benthic organisms. Coral mucus cannot be stained with the dye Alcian Blue probably due to its lack of exposed negatively charged sites (Wild et al., in preparation). Thus, our TEP measurements may underestimate the abundance of sticky marine snow aggregates especially in close vicinity to coral reefs. The correlation between TEP concentrations and suspended solids (Fig. 3) indicated that TEP was predominantly attached to, or derived from, non-fluorescent particles, and thus possibly predominantly re-suspended from the shallow sea floor. This parallels recent findings from the Lake Kineret, where a large proportion of TEP was derived from previously particulate, detrital material (Berman & Viner-Mozzini, 2001).

Marine snow aggregates reached large sizes in some inshore areas, however, the variability in size and density was high. Video records and observations on SCUBA showed individual aggregates >100 mm long at the back reef of Double Island off Cairns, together with numerous aggregates 20–40 mm in length, during Voyage 1 (described in detail in Wild, 2000). Double Island and Alexandra Reef were visited for the first time just after persistent 25–40 km h^{-1} winds subsided. During these calming conditions, slow but continuous sinking of the large aggregates was clearly visible for the divers. When these reef sites were re-visited 5 days later, TEP containing aggregates had been removed from the water column by 47 and 30%, respectively (from 449 to 160 GX l^{-1} at Double Island, and from 531 to 156 GX l^{-1} ± SE at Alexandra Reef), possibly having settled out onto the reef and surrounding sea floor. This is consistent with previous observations of marine snow sinking at ∼5 cm min^{-1} during calm periods (i.e. at currents <10 cm s^{-1}), with the sinking speed depending on the type, density, and size of the aggregates (Eisma, 1986; Alldredge & Gotschalk, 1988; Wolanski et al., 1998).

In four of the nearshore reefs where we measured marine snow, coral recruit densities are almost 3 orders of magnitude higher than juvenile densities (990 m^{-2} ± 83 SE recruits, versus 2.2 ± 0.2 m^{-2} juveniles: Fabricius, Harrington, & Smith, unpublished data), indicating high mortality rates in the early life stage of scleractinian corals. If our experimental results are indicative of ecological processes occurring in the field, the deposition of sediments enriched with marine snow may increase the mortality rates of coral recruits in coastal areas that are prone to forming marine snow.

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