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REPORT

A test of adaptive strategy theory using fifteen years of change in coral abundance

Chao-Yang Kuo[1,2] · **Morgan S. Pratchett**[1] · **Joshua S. Madin**[3] · **Andrew H. Baird**[1]

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Abstract Universal Adaptive Strategy Theory aims to predict how taxa and assemblages respond to disturbances on the basis of adaptive strategy group (ASG) membership. Here, we test such predictions using the adaptive strategy scheme for reef-building corals developed by Darling et al. (Ecol Lett 15:1378–1386, 2012) and a long-term dataset of coral assemblage structure from inshore reefs on the central Great Barrier Reef. Several disturbances including mass bleaching and tropical storms were recorded in this 15-year interval from 1998 to 2013. ASG membership did not predict how a given taxon responded to disturbance. In fact, all ASGs were on average equally affected by bleaching and a period of multiple disturbances. Furthermore, there were no consistent winners at these sites in response to the 1998 bleaching in contrast to previous work suggesting clear hierarchies in susceptibility to bleaching. In conclusion, while further efforts to re-evaluate the utility of ASGs for reef corals should be encouraged our results and a re-examination of the literature suggests that direct trait-based approaches might prove more useful when exploring how corals respond to disturbance.

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✉ Chao-Yang Kuo
cykuo.tw@gmail.com

[1] ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

[2] Biodiversity Research Center, Academia Sinica, Nankang, Taipei 11529, Taiwan

[3] Hawaiʻi Institute of Marine Biology, University of Hawaii at Manoa, Kaneohe, HI 96744, USA

Keywords Adaptive strategy · Bleaching · Coral reefs · Disturbance · Global warming · Recovery

Introduction

Adaptive strategy theory aims to reduce the number of units required to describe assemblages by grouping species based on life history strategies and functional roles. A key utility stemming from such theory is the promise to predict how taxa and assemblages respond to ecological disturbance. For example, the Universal Adaptive Strategy Theory (UAST) of Grime and Pierce (2012) identifies three adaptive groups and makes very specific predictions about the conditions under which each group should dominate and how each should respond to stress and disturbance: competitive species should benefit when disturbance and stress are low; stress-tolerant species should benefit when the intensity of stress is high; and ruderal species should benefit when disturbances are frequent (Grime and Pierce 2012).

The distinction between stress and disturbance is an important aspect of UAST (Grime and Pierce 2012): stress is defined as "the sum of many agents that limit the quantity of living matter created per unit of space and time by constraining its production"; and disturbance as "the sum of the great multiplicity of agents that limit biomass by partly or completely destroying it" (Grime and Pierce 2012). In other words, stress slows production and disturbance destroys production. Under this scheme, bleaching, flooding, and eutrophication can be defined as stresses affecting coral assemblages, whereas severe tropical storms and population outbreaks of corallivorous crown-of-thorns starfish can be defined as disturbances.

Corals often vary in their specific vulnerability to different disturbances and stresses (Van Woesik et al. 1995;

Marshall and Baird 2000; Madin et al. 2014; Pratchett et al. 2014; Hughes et al. 2018), such that changing disturbance regimes can modify the species composition of coral assemblages (McWilliam et al. 2020; Pratchett et al. 2020). The adaptive strategy approach has been used to try and explain or predict the response of coral assemblages to stress and disturbance (e. g., Darling et al. 2013; Graham et al. 2014; Sommer et al. 2014). Darling et al. (2013) found that the initial relative abundance of adaptive strategy groups (ASGs) of Darling et al. (2012) could predict change in coral assemblage structure on coastal reefs in Kenya in response to multiple stressors including fishing, which they defined as a disturbance, and a bleaching event, defined as a stress. Similarly, Graham et al. (2014) concluded that the relative abundance of Darling et al.'s (2012) ASGs was useful for distinguishing among reefs with a different disturbance history on mid-shelf reefs in the central region of the Great Barrier Reef (GBR). Specifically, the relative abundance of competitive taxa was higher on undisturbed and recovered reefs than on reefs that had not recovered from a population irruption of crown-of-thorns starfish. Sommer et al. (2014) also used Darling's scheme to compare the relative abundance of species in each adaptive group among coral assemblages along a high-latitude gradient in south-eastern Australia that included sites at the range limit of most coral species, documenting a decrease in the relative abundance of stress-tolerant species in coral assemblage at higher latitudes.

In this paper, we test whether the groups identified in Darling et al. (2012, 2013) are good predictors of the response of coral taxa to environmental stasis and change. We use a 15-year data set that documents changes in the abundance of coral genera at eight sites in the central GBR. This time-period captures a number of stresses and disturbances, including the 1998 mass-bleaching event, a tropical cyclone, and floods as well as periods of stasis when there were no disturbance events. We document winners and losers through time in order to test three sets of predictions of UAST: (1) that stress-tolerant species are less susceptible to mass bleaching compared with the other adaptive strategies; (2) competitive species increase in abundance during periods of stasis; and (3) weedy species increase in abundance after disturbances, and more-so after repeated disturbances to the same location. In addition, we tested whether the traditional bleaching hierarchies, e.g. the bleaching mortality index (BMI) (McClanahan et al. 2004), were able to reflect the mortality estimates from changes in abundance.

Materials and methods

Study site

Magnetic Island and the Palm Island group are continental islands with extensive fringing reefs located inshore within the central region of the GBR (Fig. 1). The reef environment is characterised by relatively shallow (< 15 m), highly turbid waters, with underwater visibility rarely exceeding five metres. Reefs around these islands are relatively sheltered from oceanic conditions by the expanse of the GBR lagoon, but are exposed to the influence of nearby rivers. Reef development around inshore islands on the GBR is often patchy, giving way to soft sediments as shallow as eight metres on landward reefs. Coral assemblages were monitored at two locations in each island group: Nelly Bay (−19.167, 146.850) and Geoffrey Bay (−19.155, 146.861) at Magnetic Island; and Little Pioneer Bay (−18.594, 146.485) and southeast Pelorus (−18.560, 146.500) at the Palm Islands. Two depths (shallow (S): 2–4 m; deep (D): 5–8 m) were surveyed at each location to give a total of eight sites.

Survey method

Between six and nine surveys were conducted at each site between 1998 and 2013. The first set of surveys was conducted in February/March 1998 during the mass bleaching event (Baird and Marshall 1998; Marshall and Baird 2000); the second set of surveys was conducted in September/October 1998 by which time the vast majority of the coral had recovered or died (Baird and Marshall 2002). Between four and six replicate 15 m × 0.5 m belt transects were used at each site on each survey. The abundance of all hard and soft corals with a maximum diameter greater than 5 cm within the belt transects was recorded. Hard corals include Scleractinia and Hydrocorallina, whereas soft corals are limited to *Lobophytum*, *Sarcophyton*, and *Sinularia*. All colonies were identified in the field to genus following Veron (2000) for the scleractinian corals and Fabricius and Aldersdale (2001) for the soft corals. Hard coral genera were further classified into ASGs following Darling et al (2012, 2013; Table 1). We used colony abundance instead of the more commonly used metric of coral cover because it provided a much better estimate of population-level mortality. The raw data are accessible from Baird et al. (2020).

Change in coral abundance through time

Change in the mean abundance of corals through time was tested using one-way ANOVA with Tukey post-hoc tests to identify marked temporal changes in coral abundance.

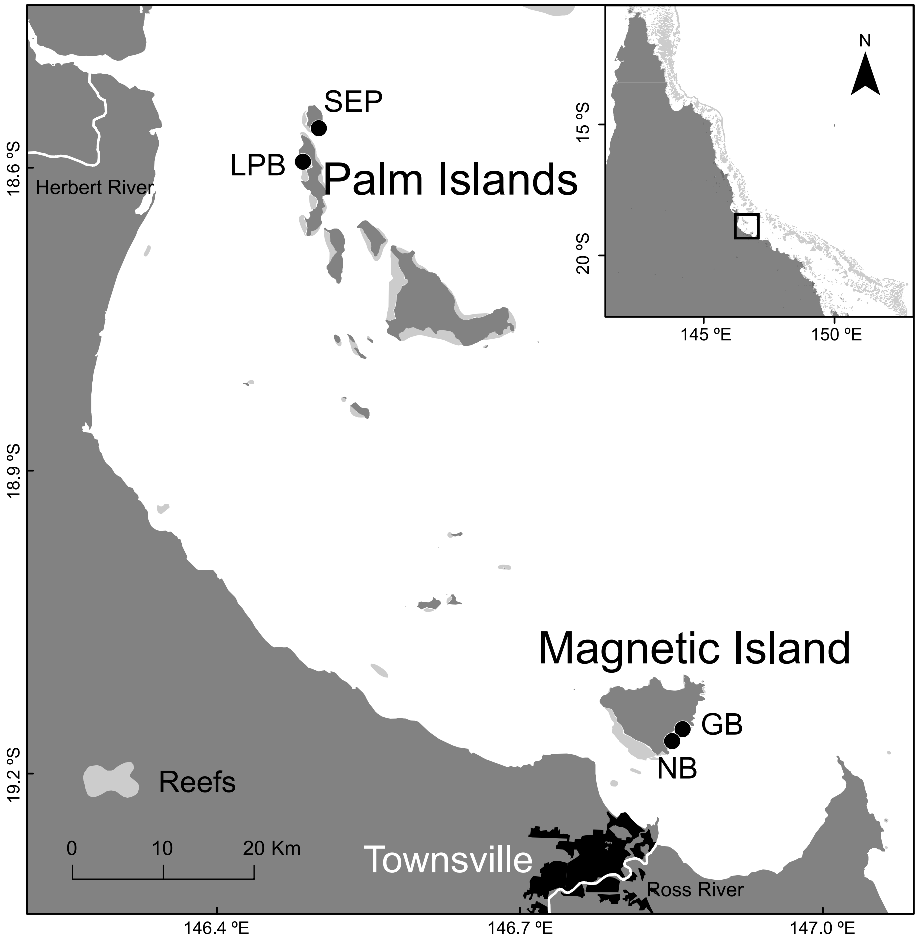

Fig. 1 Location of survey sites, including Nelly Bay (NB); Geoffrey Bay (GB); Little Pioneer Bay (LPB); and southeast Pelorus (SEP) in the central GBR region

Assumptions of normality of residuals and homogeneity of variances were assessed by reviewing plots of residuals against fitted values and Q–Q plots. A log-transformation was applied if violations of assumptions were detected.

Disturbance regime through the course of the study

The period of the study included a number of potential stresses and disturbances, including cyclones, bleaching, floods, and low tide events. These multiple stressors affected each site to a different and often unknown level (Table 2). In order to test the response of the taxa and ASGs, we defined three time-intervals based on the timing of disturbances:

1. Stress—a bleaching event (March 1998);
2. Recovery—no stress or disturbance. There was a brief period free of stress and disturbance on Magnetic Island (October 1998 to April 2000) and in the Palm Islands (December 2001 to March 2005). There were no periods without disturbance at the regional scale;
3. Multiple-disturbances—the total time interval of the study (March 1998 to 2012/13) during which there were multiple disturbance and stress events

The response of taxa in the different time intervals

Changes in the abundance of the taxa during each of the three time-intervals were explored at both the site and regional level (i.e. all sites pooled) using Cohen's *d* effect size, which is defined as the difference between two means of each time point, $\bar{x}_1$ and $\bar{x}_2$, divided by a pooled standard deviation, s, for the data and was estimated as follows (Cohen 1988):

Table 1 Adaptive strategy groups for each genus in the study based on Darling et al. (2012, 2013)

Genus	Darling group	Genus	Darling group
Acanthastrea	Stress-tolerant	*Merulina*	Generalist
Acropora	Competitive	*Millepora*	Unknown
Alveopora	Stress-tolerant	*Montastrea*	Stress-tolerant
Astreopora	Stress-tolerant	*Montipora*	Generalist
Caryophyllia	Unknown	*Moseleya*	Unknown
Coeloseris	Unknown	*Mycedium*	Generalist
Coscinaraea	Unknown	*Oulophyllia*	Stress-tolerant
Cyphastrea	Stress-tolerant	*Oxypora*	Unknown
Diploastrea	Stress-tolerant	*Pachyseris*	Generalist
Echinophyllia	Stress-tolerant	*Pavona*	Generalist
Echinopora	Generalist	*Pectinia*	Unknown
Favia	Stress-tolerant	*Platygyra*	Stress-tolerant
Favites	Stress-tolerant	*Plesiastrea*	Stress-tolerant
Fungiidae	Stress-tolerant	*Pocillopora*	Weedy
Galaxea	Stress-tolerant	*Porites*	Stress-tolerant
Goniastrea	Stress-tolerant	*Psammocora*	Generalist
Goniopora	Unknown	*Sarcophyton*	Unknown
Hydnophora	Generalist	*Scolymia*	Stress-tolerant
Isopora	Unknown	*Seriatopora*	Weedy
Leptastrea	Weedy	*Sinularia*	Unknown
Leptoria	Stress-tolerant	*Stylocoeniella*	Unknown
Leptoseris	Unknown	*Stylophora*	Weedy
Lobophyllia	Stress-tolerant	*Symphyllia*	Stress-tolerant
Lobophytum	Unknown	*Turbinaria*	Competitive

$$d = \frac{\overline{x}_2 - \overline{x}_1}{s}$$

$$s = \sqrt{\frac{\left(n_1 - 1\right)s_1^2 + \left(n_2 - 1\right)s_2^2}{n_1 + n_2 - 2}}$$

$$s_1^2 = \frac{1}{n_1 - 1} \sum_{i=1}^{n_1} \left(x_{1,i} - \overline{x}_1\right)^2$$

Cohen's d takes into account the variance in the data in addition to the difference between the means (Cohen 1988), which addresses potential sampling issues with for taxa with low abundances.

Winners were defined as taxa that increase in abundance in the given time interval and had an effect size $> +0.8$ which is described in the literature as a very strong effect (Cohen 1988). The strong effect means that colony abundance on 79% of transects sampled in the second time point was higher than the average colony abundance from transects sampled in the first time point. Losers were defined as taxa that decreased in abundance in the given time-interval and had an effect size < -0.8.

Bleaching response index vs. response as estimated by change in effect size

The bleaching mortality index (BMI) was developed by McClanahan et al. (2004) as a metric for comparing bleaching susceptibility among genus based on the categorical bleaching categories of Marshall and Baird (2000). The relationship between BMI and Cohen's d was tested using linear regression.

Results

Changes in abundance through time

At the regional scale, there have been significant changes in coral abundance over the 15-year time period. The 1998 bleaching caused a 50% reduction in the mean abundance of corals. A gradual increase until 2005 was followed by a decline in abundance towards the lowest coral abundance in the study period in 2012/13 (Fig. 2; Table 3, S1). Seven of the eight sites have experienced significant changes in coral abundance, including at least one period of increase and decrease (Fig. 3; Table 3, S2–S9). Bleaching in 1998 caused significant declines in abundance at six of the eight sites (Fig. 3; Table 3). The only sites unaffected in terms of the overall abundance of coral were the sites at southeast Pelorus. Increases in coral abundance were evident at all sites following the bleaching in 1998. However, recovery

Table 2 History of disturbance affecting the study sites during study period

Date	Incident	Nelly Bay	Geoffrey Bay	Little Pioneer Bay	southeast Pelorus	References
Mar-1998	Bleaching	Yes	Yes	Yes	Yes	Marshall and Baird (2000), Berkelmans et al. (2004)
Mar-2002	Bleaching	Yes	Yes	Unknown	Unknown	Berkelmans et al. (2004)
Sep-2005	Low tides	Unknown	Unknown	Yes	Unknown	Anthony and Kerswell (2007)
Summer-2009	Flood—Ross River	Yes	Yes	Unknown	Unknown	Haapkylä et al. (2011)
2010–2011	Flood—Burdekin River	Unknown	Unknown	Unknown	Unknown	Bainbridge et al. (2012)
Feb-2011	Cyclone Yasi	Unknown	Unknown	Unknown	Yes	Lukoschek et al. (2013)

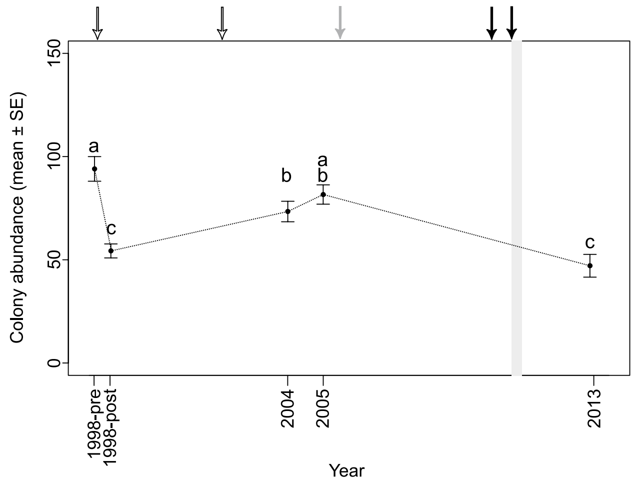

Fig. 2 Temporal changes in coral colony abundance at regional scale, all sites pooled together, in the central GBR region from 1998 to the last survey in 2013. The five time points are the surveys which were conducted at all eight sites. Arrows indicate disturbances, including two bleaching events (1998 and 2002, white), one low tide event (2005, grey), two flood events (2009, 2010–2011, black). The grey bar indicates tropical cyclone Yasi in 2011. Letters above dots indicate significant groupings by Tukey's post hoc test at different surveys

at Magnetic Island sites was set back by another bleaching event in 2002 followed by subsequent multiple stressors. This has resulted in significantly fewer corals on Magnetic Island in 2013 compared to 1998, at three of the four sites, except GB-D (Fig. 3; Table 3). Bleaching in 2002 did not appear to affect the sites in Palm Island where coral abundance peaked in 2004/5. Since then, Palm Island sites have experienced multiple stressors, including cyclone Yasi in 2011, leading to significant declines in coral abundance. There were less corals at all sites in the Palm Islands in 2012 compared to 1998 (Fig. 3; Table 3).

Response of taxa to bleaching in 1998

Most taxa decreased in abundance in response to bleaching. At a regional scale, 37 of the 48 taxa declined in abundance (Table 4, S1). Similarly, at six of the eight sites, most taxa declined in abundance (Table 4, S2–S9). Based on the effect size, losers greatly outnumbered winners at all sites (Table 4, S2–S9).

The losers varied greatly among sites (Table 5); however, some taxa were losers at multiple sites. For example, *Montipora*, *Acropora*, *Cyphastrea*, *Turbinaria*, *Porites*, *Favia*, *Gonipora*, *Galaxea*, *Pocillopora*, *Sinularia* and *Montastrea* were always among the losers at the five most affected sites (Table 5). *Seriatopora* and *Stylophora* were consistent losers at the sites that did not suffer large declines in total coral abundance (i.e. SEP-S & SEP-D). Losers came from all ASGs at both the regional scale (Fig. 4) and at most sites (Fig. 5).

The winners in response to bleaching were very few (Table 6). At the regional scale there were no winners (Table 6). At the site scale *Platygyra* and *Sarcophyton* were winners at two sites and the following taxa were winners at one site; *Alveopora, Astreopora, Galaxea, Montipora, Oulophyllia, Pachyseris, Leptastrea* and *Leptoseris* (Table 6). Winners were either stress-tolerant species or generalist taxa (Figs. 4, 5).

Response of taxa to multiple disturbances

The response of taxa to multiple disturbances was very similar to the response to bleaching except there were even fewer winners and more losers, particularly at the sites at southeast Pelorus (Tables 4, 5, 6, S2–S9). At the regional scale, competitive and weedy taxa were more susceptible to multiple disturbances than stress-tolerant and generalist species (Fig. 4, S1). At the site scale, losers came from all ASGs (Fig. 6). At the regional scale there were no winners (Table 4). Winners at the site scale were either stress-tolerant

Table 3 One-way ANOVA testing for difference in mean coral abundance through time at eight sites in the central Great Barrier Reef region from 1998 to 2012/13

Site (abbreviation)		Was it affected by the 1998 bleaching event?
Regional scale	$F = 15.06$, $df = 4, 234$, $P < 0.001$	Yes
Nelly Bay-2 m (NB-S)	$F = 13.16$, $df = 5, 28$, $P < 0.001$	Yes
Nelly Bay-6 m (NB-D)	$F = 35.88$, $df = 5, 31$, $P < 0.001$	Yes
Geoffrey Bay-2 m (GB-S)	$F = 18.28$, $df = 5, 28$, $P < 0.001$	Yes
Geoffrey Bay-6 m (GB-D)	$F = 2.75$, $df = 5, 32$, $\mathrm{P} = 0.036$	Yes
Little Pioneer Bay-2 m (LPB-S)	$F = 4.97$, $df = 8, 46$, $\mathrm{P} < 0.001$	Yes
Little Pioneer Bay-6 m (LPB-D)	$F = 2.60$, $df = 8, 45$, $\mathrm{P} = 0.020$	No
southeast Pelorus -4 m (SEP-S)	$F = 34.31$, $df = 6, 33$, $P < 0.001$	No
southeast Pelorus -6 m (SEP-D)	$F = 14.58$, $df = 6, 30$, $P < 0.001$	No

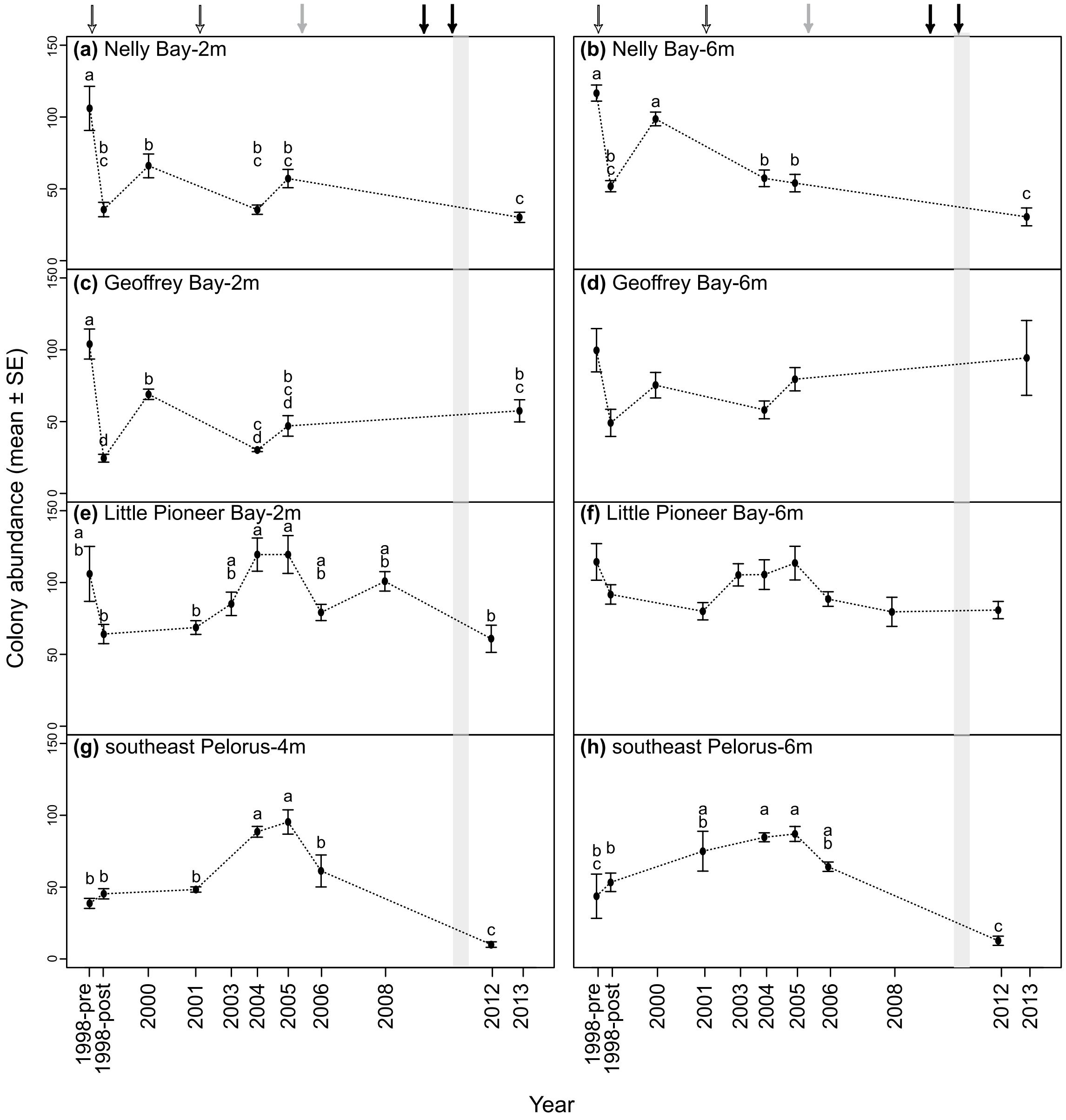

Fig. 3 Temporal changes in average coral colony abundance (mean ± SE) at 8 sites in the central GBR region from 1998 to 2013. Sites include Nelly Bay 2 m (**a**) 6 m (**b**), Geoffrey Bay 2 m (**c**) 6 m (**d**), Little Pioneer Bay 2 m (**e**) 6 m (**f**), and southeast Pelorus 4 m (**g**) 6 m (**h**). Arrows indicated disturbances including two bleaching events (1998 and 2002, white), one low tide event (2005, grey), two flood events (2009, 2010–2011, black). The grey bar indicates tropical cyclone Yasi in 2011. Letters above dots indicate significant groupings by one-way ANOVA, Welch's *F* test and Tukey's post hoc test at different surveys

species (*Porites*, Fungiidae, and *Favites*) or generalists (*Mycedium* and *Pavona*; Figs. 4, 6).

Response of taxa to periods of no disturbance or stress

Winners outnumbered losers in the recovery periods at most sites (Table 4, S2–S9). The losing taxa varied greatly among sites with only *Montastrea* losing at more than one site (Table 5). A number of taxa were consistent winners. In particular, *Montipora* and *Acropora* were winners at four sites and *Turbinaria*, *Favia*, *Favites*, *Sinularia*, *Porites* and the Fungiidae at two or more (Table 5). Losers were mostly stress-tolerant species and generalist (Fig. 7) but also included weeds and one competitor at one site (*Turbinaria* at LPB-D). Winners included taxa from all ASGs (Fig. 7).

Table 4 Summary of changes in generic richness at each site following bleaching, multiple disturbances and during a period of no disturbance (recovery)

Site	Period	Taxa	Decrease	Increase	Extinction	Coloniser	Losers	Winners
Region	Bleach	48	37	11	0	0	13	0
Region	multiple	48	36	12	0	5	13	0
Nelly Bay-2 m	Bleach	23	21	2	11	2	14	1
Nelly Bay-6 m	Bleach	30	27	3	13	2	12	0
Geoffrey Bay-2 m	Bleach	22	22	0	14	3	14	0
Geoffrey Bay-6 m	Bleach	33	27	6	7	5	16	0
Little Pioneer Bay-2 m	Bleach	37	31	7	10	4	15	3
Little Pioneer Bay-6 m	Bleach	38	25	13	4	5	8	5
southeast Pelorus-4 m	Bleach	29	14	15	8	4	6	2
southeast Pelorus-6 m	Bleach	23	10	13	4	8	4	1
Nelly Bay-2 m	Multiple	23	22	1	11	1	13	0
Nelly Bay-6 m	Multiple	30	25	5	14	4	12	0
Geoffrey Bay-2 m	Multiple	22	18	4	13	2	11	0
GeoffreyBay-6 m	Multiple	33	24	9	7	6	11	2
Little Pioneer Bay-2 m	Multiple	37	27	10	9	3	14	1
Little Pioneer Bay-6 m	Multiple	38	20	18	3	3	9	1
southeast Pelorus-4 m	Multiple	29	25	4	18	1	14	0
southeast Pelorus-6 m	Multiple	23	21	2	10	6	17	1
Nelly Bay-2 m	Recovery	15	6	9	3	8	2	4
Nelly Bay-6 m	Recovery	19	7	12	4	11	2	6
Geoffrey Bay-2 m	Recovery	11	4	7	2	10	2	3
Geoffrey Bay-6 m	Recovery	32	14	18	6	6	1	3
Little Pioneer Bay-2 m	Recovery	25	4	21	0	8	2	10
Little Pioneer Bay-6 m	Recovery	38	14	24	4	6	3	6
southeast Pelorus-4 m	Recovery	19	11	8	3	11	4	4
southeast Pelorus-6 m	Recovery	25	15	10	3	2	1	3

Bleaching response index vs response as estimated by change in effect size

There was no correlation between susceptibility to bleaching as determined by the bleaching response index (BMI) and change in abundance as estimated by Cohen's *d* effect size ($R^2 = 0.003$, $p = 0.362$) (Fig. 8).

Discussion

No taxa were winners during the 15-year period of multiple stressors. At the regional scale, all taxa were less abundant in 2013 than in 1998, which was similar to studies conducted on reefs nearby in the same period (e.g., Torda et al. 2018). Despite these changes and a 50% reduction in coral abundance between 1998 and 2013, there have been no extinctions at the regional scale. Therefore, multiple stressors on inshore reefs on the GBR have resulted in a lower abundance of all corals rather than causing major shifts in assemblage structure. A least one cycle of recovery in abundance has occurred at all sites, with some sites experiencing up to three periods of recovery, suggesting the ecological processes necessary for recovery remain essentially intact. The poor status of these sites at the end of the study is therefore attributable mainly to the recent incidence of disturbances, especially cyclone Yasi (in February 2011), rather than systematic declines in the abundance of corals. Indeed, coral abundance at most sites was increasing until mass bleaching events in March 2016 and 2017 (unpublished data). Nonetheless, recent research suggests that the disturbance regime on reefs has transitioned into an era where climate change and other human-induced changes will predominate over natural disturbances (Hughes et al. 2017; Tan et al. 2018). Furthermore, the intensity of cyclones is predicted to increase in response to ongoing climate change (Knutson et al. 2010). This 15-year period might therefore be a guide to the future status of coral reefs.

Losers greatly outnumbered winners in response to bleaching. This is not surprising because the time interval between censuses was six months and therefore the opportunity to recruit into the sample population (i.e. colonies with a maximum diameter greater than 5 cm) is mostly limited to those species susceptible to fission, such as *Platygyra* (Babcock 1991) and *Sarcophyton*. Nonetheless, these results support recent findings that very few taxa are winners when

Table 5 The losers during each of the three periods at the regional and site scale

Site	Period	Losers
Region	Bleach	*Cyphastrea*, *Montipora*, *Favia*, *Pocillopora*, *Stylophora*, *Acropora*, *Lobophyllia*, *Goniastrea*, *Turbinaria*, *Galaxea*, *Sinularia*
Region	Multiple disturbance	*Acropora*, *Favia*, *Galaxea*, *Montipora*, *Millepora*, *Pectinia*, *Cyphastrea*, *Seriatopora, Pocillopora*, *Sarcophyton, Stylophora*, *Sinularia*, *Gonipora*, *Lobophyllia*, *Turbinaria*,
Nelly Bay-2 m	Bleach	*Montipora*, *Acropora*, *Cyphastrea*, *Turbinaria*, *Porites*, *Favia*, *Gonipora*, *Goniastrea*, *Pavona*, *Alveopora*, *Galaxea*, *Plesiastrea*, *Leptoseris*, *Lobophyllia*, *Psammocora*
Nelly Bay-6 m	Bleach	*Cyphastrea*, *Turbinaria*, *Acropora*, *Favia*, *Montipora*, *Goniopora*, *Hydnophora*, *Galaxea*, *Porites*, *Goniastrea*, *Moseleya*, *Oxypora*
Geoffrey Bay-2 m	Bleach	*Montipora*, *Favia*, *Acropora*, *Galaxea*, *Stylophora*, *Cyphastrea*, *Turbinaria*, *Favites*, *Gonipora*, *Porites*, *Goniastrea*, *Lobophyllia*, *Pocillopora*, *Moseleya*
Geoffrey Bay-6 m	Bleach	*Lobophyllia*, *Oxypora*, *Merulina*, *Montipora*, *Favia*, *Goniastrea*, *Stylophora*, *Sarcophyton*, *Moseleya*, *Lobophytum*, *Pocillopora*, *Porites*, *Pachyseris*, *Galaxea*, *Mycedium*
Little Pioneer Bay-2 m	Bleach	*Sinularia*, *Goniopora*, *Montipora*, *Pectinia*, *Pocillopora*, *Cyphastrea*, *Millepora*, *Acropora*, *Goniastrea*, *Merulina*, *Favia*, *Montastrea*, *Favites*, *Acanthastrea*, *Echinophyllia*
Little Pioneer Bay-6 m	Bleach	*Sinularia*, *Montipora*, *Pavona*, *Lobophyllia*, *Acanthastrea*, *Echinopora*, *Favia*, *Goniastea*
southeast Pelorus-4 m	Bleach	*Isopora*, *Leptoria*, *Pocillopora*, *Montastrea*, *Seriatopora*, *Stylophora*
southeast Pelorus-6 m	Bleach	*Seriatpora*, *Stylophora*, *Goniastrea*, *Leptastrea*
Nelly Bay-2 m	Multiple	*Porites*, *Acropora*, *Montipora*, *Cyphastrea*, *Goniastrea*, *Favia*, *Turbinaria*, *Favites*, *Gonipora*, *Galaxea*, *Coscinareae*, *Plesiastrea*, *Lobophyllia*
Nelly Bay-6 m	Multiple	*Acropora*, *Montipora*, *Galaxea*, *Turbinaria*. *Cyphastrea*, *Gonipora*, *Favia*, *Hydnophora*, *Goniastrea*, *Montastrea*, *Pectinia*, *Oxypora*,
Geoffrey Bay-2 m	Multiple	*Favia*, *Acropora*, *Galaxea*, *Stylophora*, *Turbinaria*, *Cyphastrea*, *Favites*, *Moseleya*, *Lobophyllia*, *Pocillopora*, *Porites*
Geoffrey Bay-6 m	Multiple	*Sarcophyton*, *Lobophyllia*, *Lobophytum*, *Favia*, *Goniastrea*, *Symphyllia*, *Oxypora*, *Moseleya*, *Stylopora*, *Pocillopora*, *Oulophyllia*,
Little Pioneer Bay-2 m	Multiple	*Gonipora*, *Montipora*, *Cyphastrea*, *Pectinia*, *Millepora*, *Favites*, *Sinularia*, *Favia*, *Merulina*, *Lobophyllia*, *Pocillopora*, *Seriatopora*, Fungiidae, *Pachyseris*, *Acanthastrea*
Little Pioneer Bay-6 m	Multiple	*Cyphastrea*, *Pectinia*, *Montipora*, *Symphyllia*, *Echinopora*, *Sinularia*, *Galaxea*, *Millepora*, *Astreopora*,
southeast Pelorus-4 m	Multiple	*Leptoria*, *Acropora*, *Pocillopora*, *Sinularia*, *Lobophytum*, *Favia*, *Isopora*, *Favites*, *Merulina*, *Hydnophora*, *Seriatopora*, *Stylophora*, *Goniopora*, *Porites*
southeast Pelorus-6 m	Multiple	*Sarcophyton*, *Seriatopora*, *Acropora*, *Echinopora*, *Favia*, *Pocillopora*, *Galaxea*, *Platygyra*, *Stylophora*, *Lobophytum*, *Montipora*, *Leptoria*, *Hydnophora*, *Merulina*, *Millepora*, *Sinularia*
Nelly Bay-2 m	Recovery	*Coscinaraea*, *Leptoseris*
Nelly Bay-6 m	Recovery	*Leptoria*, *Montastrea*,
Geoffrey Bay-2 m	Recovery	*Seriatopora*, *Leptoria*
Geoffrey Bay-6 m	Recovery	*Montastrea*
Little Pioneer Bay-2 m	Recovery	*Symphyllia*, *Platygyra*
Little Pioneer Bay-6 m	Recovery	*Echinophyllia*, *Montastrea*, *Turbinaria*
southeast Pelorus-4 m	Recovery	*Montastrea*, *Acanthastrea*, *Astreopora*, *Goniastrea*
southeast Pelorus-6 m	Recovery	*Favites*

bleaching events are severe (Hughes et al. 2017). In addition, traditional bleaching hierarchies based on a single census of bleaching status within populations during a bleaching event (e.g. Marshall and Baird 2000; McClanahan et al. 2004) do not reflect those based on mortality estimates from changes in abundance (Fig. 8). In particular, a number of taxa that rarely bleach, for example, *Cyphastrea* spp. and *Alveopora* spp. suffered high rates of mortality (Marshall and Baird 2000; McClanahan 2004; Fig. 8). These results suggest that some taxa that are susceptible to bleaching do not present with symptoms typical of bleaching, such as loss of symbionts and consequent paling of the colony. Accurate estimates of the effects of thermal anomalies on reefs, therefore, require individuals to be tagged and followed through time (e.g. Baird and Marshall 2002). The fact that very few taxa can cope with thermal stress is probably due to the fact that severe thermal anomalies in the ocean are a relatively recent phenomenon (Spalding and Brown 2015), and therefore, corals have not had the chance to adapt to this form of stress.

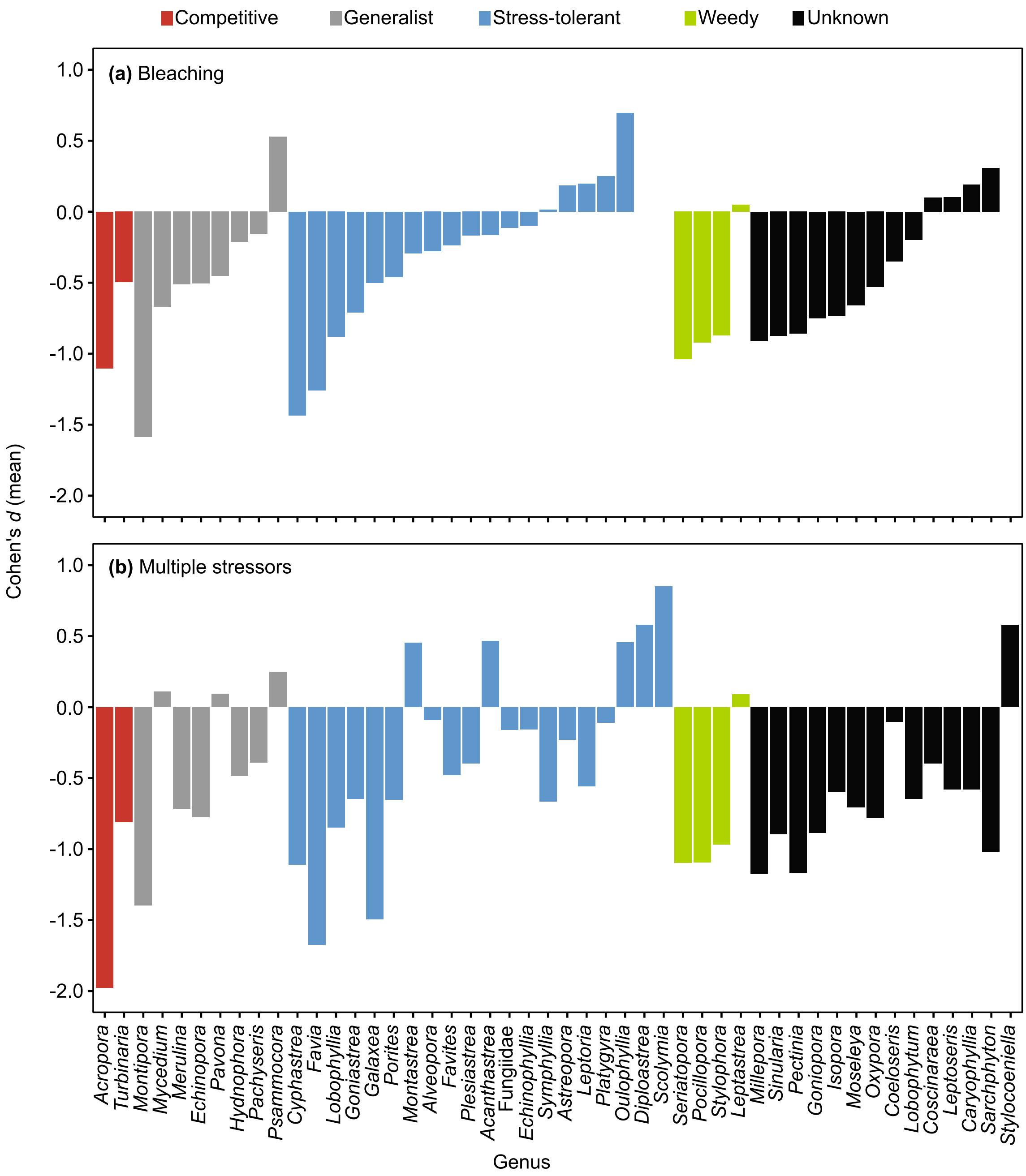

Fig. 4 Effect size by taxa for bleaching (**a**) and multiple disturbances (**b**) at regional scale. Colours indicate the ASG; competitive (red), generalist (grey), stress-tolerant (blue), weedy (green) and unknown (black)

Few predictions of UAST with respect to how taxa should respond to stress and disturbance are supported by these data. While the two competitive-taxa, *Acropora* and *Turbinaria*, were among the winners at the site level during periods of recovery, winners also included multiple genera from the other groups (Table 6). Indeed, there was a large range of responses among taxa within most adaptive groups. For example, the stress-tolerant taxa *Cyphastrea*, *Favia* and *Goniastrea* were consistently among the biggest losers at many sites following bleaching (Fig. 5). Similarly, the same taxa responded in different ways to the same stress at different sites. For example, *Montipora* was consistently among the losers in response to bleaching, however, at SEP-D it was a winner (Tables 4, 5). This is evidence of marked response diversity within some species-rich genera (e.g., *Montipora)*, suggesting that higher taxonomic groupings or adaptive groups are inappropriate for representing the vulnerability and responses of corals to disturbances and stresses.

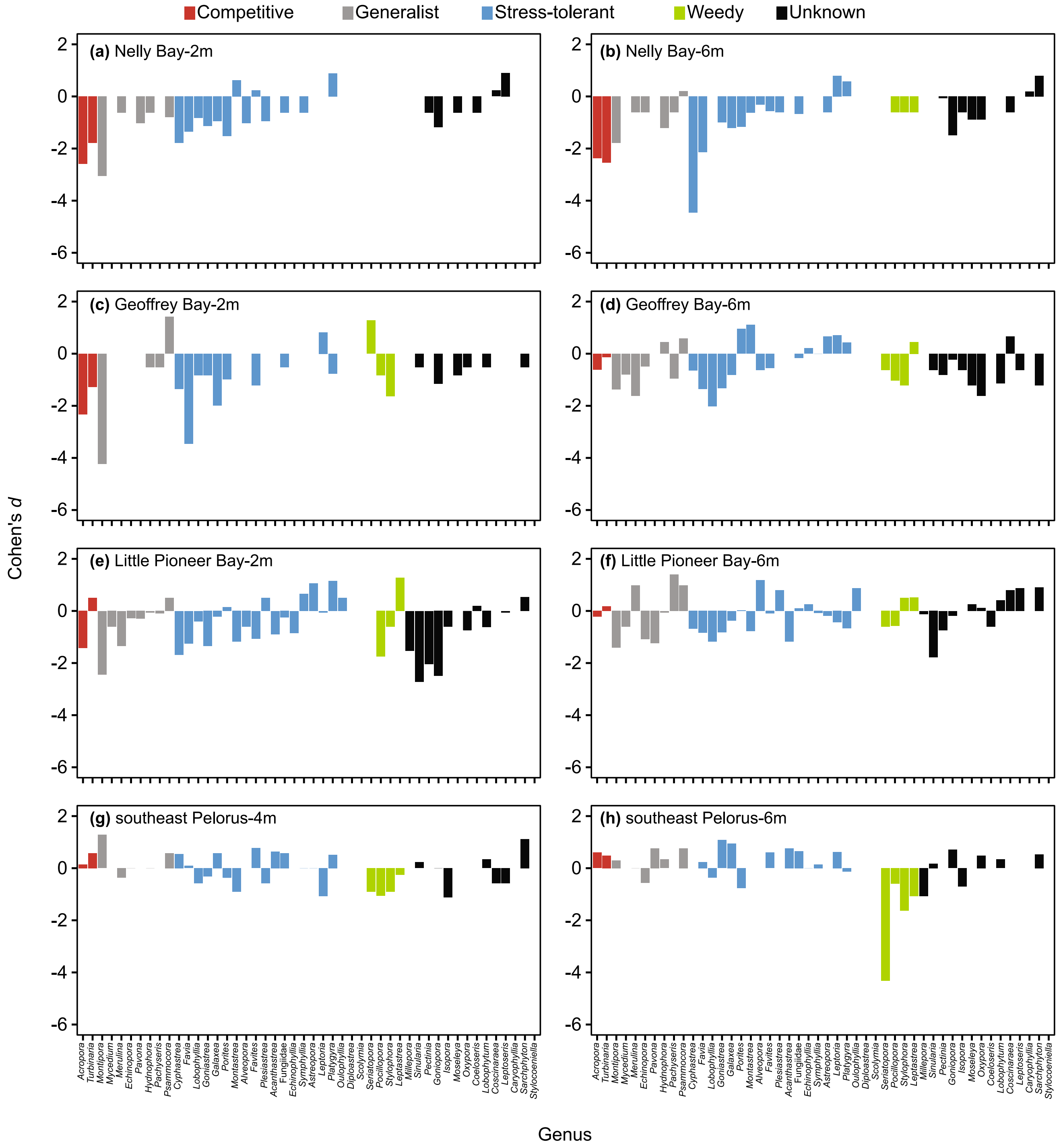

Fig. 5 Effect size by taxa for bleaching event. Sites include Nelly Bay 2 m (**a**) 6 m (**b**), Geoffrey Bay 2 m (**c**) 6 m (**d**), Little Pioneer Bay 2 m (**e**) 6 m (**f**), and southeast Pelorus 4 m (**g**) 6 m (**h**). Colours indicate the ASG; competitive (red), generalist (grey), stress-tolerant (blue), weedy (green) and unknown (black)

Indeed, there are few traits that are similar among species within most genera, in particular species-rich genera like the *Acropora*, *Montipora* and *Porites* (Madin et al. 2016). One prediction of UAST supported by these data is that it is not possible for organisms to adapt to a high frequency of both stress and disturbance (Grime and Pierce 2012). Indeed, there appear to be no true weedy species in the sessile anthozoa on the GBR. In other words, species capable of a rapid increase in abundance in response to disturbance are

Table 6 The winners during each of the three periods at the regional and site scale

Site	Period	Winners
Region	Bleach	None
Region	Multiple	*Scolymia*
Nelly Bay-2 m	Bleach	*Platygyra*
Nelly Bay-6 m	Bleach	None
Geoffrey Bay-2 m	Bleach	None
Geoffrey Bay-6 m	Bleach	None
Little Pioneer Bay-2 m	Bleach	*Leptastrea*, *Platygyra*, *Astreopora*
Little Pioneer Bay-6 m	Bleach	*Pachyseris*, *Alveopora*, *Sarcophyton*, *Oulophyllia*, *Leptoseris*
southeast Pelorus-4 m	Bleach	*Montipora*, *Sarcophyton*
southeast Pelorus-6 m	Bleach	*Galaxea*
Nelly Bay-2 m	Multiple	None
Nelly Bay-6 m	Multiple	None
Geoffrey Bay-2 m	Multiple	None
Geoffrey Bay-6 m	Multiple	*Porites*, Fungiidae
Little Pioneer Bay-2 m	Multiple	*Pavona*
Little Pioneer Bay-6 m	Multiple	*Mycedium*
southeast Pelorus-4 m	Multiple	None
southeast Pelorus-6 m	Multiple	*Favites*
Nelly Bay-2 m	Recovery	*Montipora*, *Acropora*, *Goniastrea*, *Turbinaria*
Nelly Bay-6 m	Recovery	*Favia*, Fungiidae, *Montipora*, *Galaxea*, *Turbinaria*, *Acropora*, *Favites*, *Porites*, *Cyphastrea*
Geoffrey Bay-2 m	Recovery	*Montipora*, *Turbinaria*, *Acropora*
Geoffrey Bay-6 m	Recovery	*Montipora*, *Sinularia*, Fungiidae
Little Pioneer Bay-2 m	Recovery	*Pectinia*, *Acropora*, *Porites*, *Lobophyllia*, *Echinophyllia*, *Favites*, *Echinopora*, *Pavona*, *Astreopora*, *Sarcophyton*
Little Pioneer Bay-6 m	Recovery	*Sinularia*, *Favia*, *Porites*, *Echinopora*, *Sarcophyton*, *Galaxea*
southeast Pelorus-4 m	Recovery	*Acropora*, *Coeloseris*, *Favia*, *Symphyllia*
southeast Pelorus-6 m	Recovery	*Pocillopora*, *Platygyra*, *Leptastrea*

rare on coral reefs, unlike the numerous species of weeds in terrestrial environments (Grime and Pierce 2012).

The relative abundance of the adaptive strategies in the initial assemblages was not a good predictor of the trajectory of the assemblage in response to stress or multiple disturbances. Indeed, seven of the eight sites were equally degraded in the 15 years of the study despite large differences in initial assemblage structure. In particular, the *Acropora* dominated assemblages at southeast Pelorus were the least affected by bleaching (Fig. 3), at least with respect to changes in abundance. This is despite very high levels of mortality in tagged colonies of *Acropora* at southeast Pelorus (Baird and Marshall 2002). This again suggests that there are important differences in the response to bleaching among species within genera and categorising higher taxonomic groups to specific adaptive strategies is inappropriate.

A closer look at previous research also suggests that ASGs rarely behave as predicted (see also Zinke et al. 2018). For example, Darling et al. (2013) tested the response of ASGs to bleaching and fishing. In contrast to predictions, weedy species did not consistently benefit from disturbance, competitive species did not benefit from periods free of disturbance and the responses of stress tolerant species were context dependent (e.g., big declines were observed on unfished reefs, but no declines on fished reefs). The only response consistent with the theory was that competitors were more susceptible to the chronic disturbance in the form of fishing than stress-tolerant and weedy species. However, all the competitive species in this study were either branching *Acropora* spp. or *Pocillopora* spp. suggesting that classification of species based on morphology would have been equally as informative. Similarly, Graham et al. (2014) concluded that the relative abundance of ASGs was useful for distinguishing among reefs with a different disturbance history on the GBR. However, the only locally abundant species classified as competitors were *Acropora* spp. Therefore, these reefs could equally well have been distinguished by classifying taxa as *Acropora* vs non-*Acropora*. Sommer et al. (2014) also used an adaptive strategy scheme to compare the relative abundance of species in each group among coral assemblages along a high-latitude gradient in south-eastern Australia. The only clear trend was a decrease in the relative

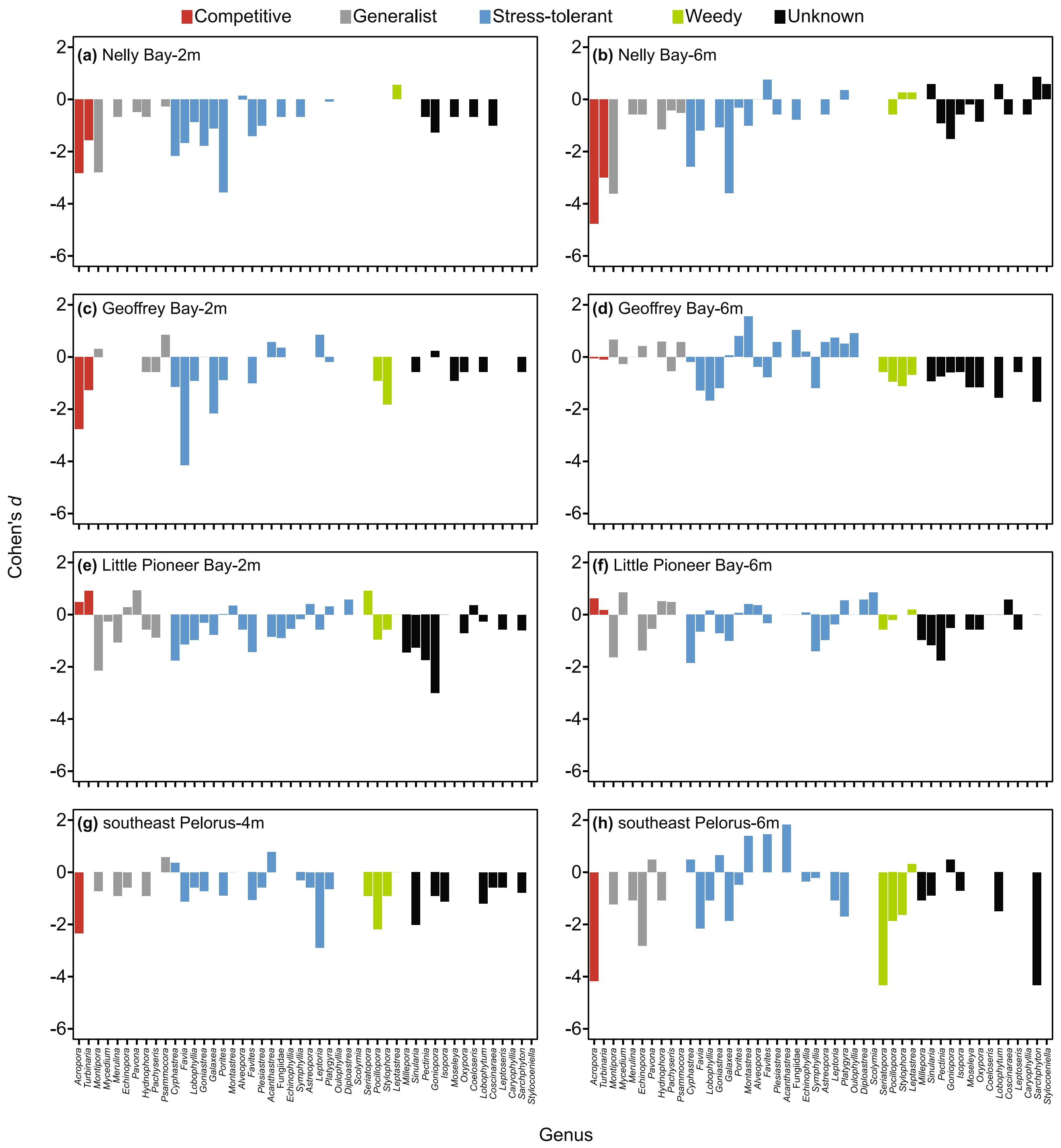

Fig. 6 Effect size by taxa for multiple disturbances. Sites include Nelly Bay 2 m (**a**) 6 m (**b**), Geoffrey Bay 2 m (**c**) 6 m (**d**), Little Pioneer Bay 2 m (**e**) 6 m (**f**), and southeast Pelorus 4 m (**g**) 6 m (**h**). Colours indicate the ASG; competitive (red), generalist (grey), stress-tolerant (blue), weedy (green) and unknown (black)

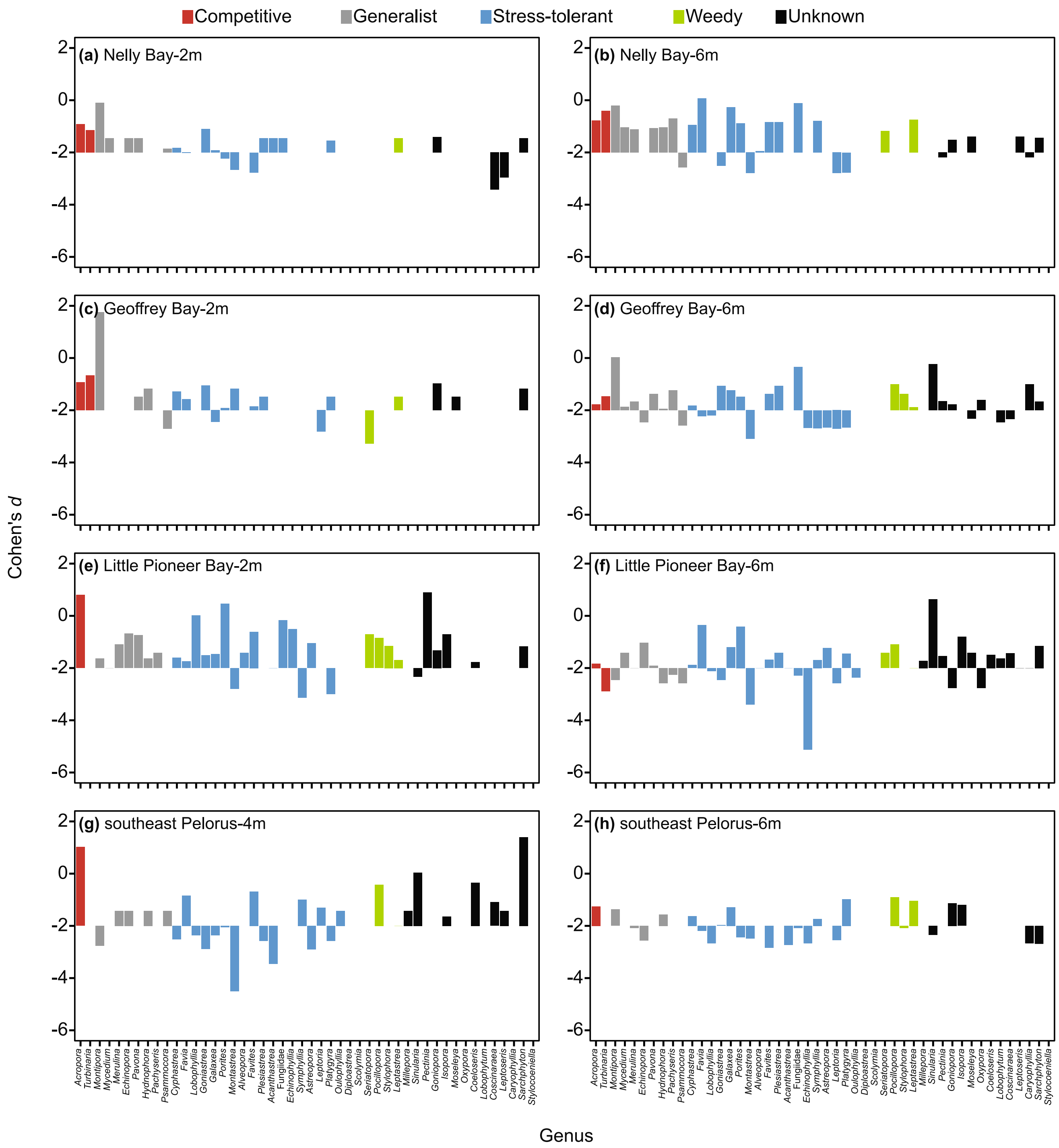

Fig. 7 Effect size by taxa for recover period. Sites include Nelly Bay 2 m (**a**) 6 m (**b**), Geoffrey Bay 2 m (**c**) 6 m (**d**), Little Pioneer Bay 2 m (**e**) 6 m (**f**), and southeast Pelorus 4 m (**g**) 6 m (**h**). Colours indicate the ASG; competitive (red), generalist (grey), stress-tolerant (blue), weedy (green) and unknown (black)

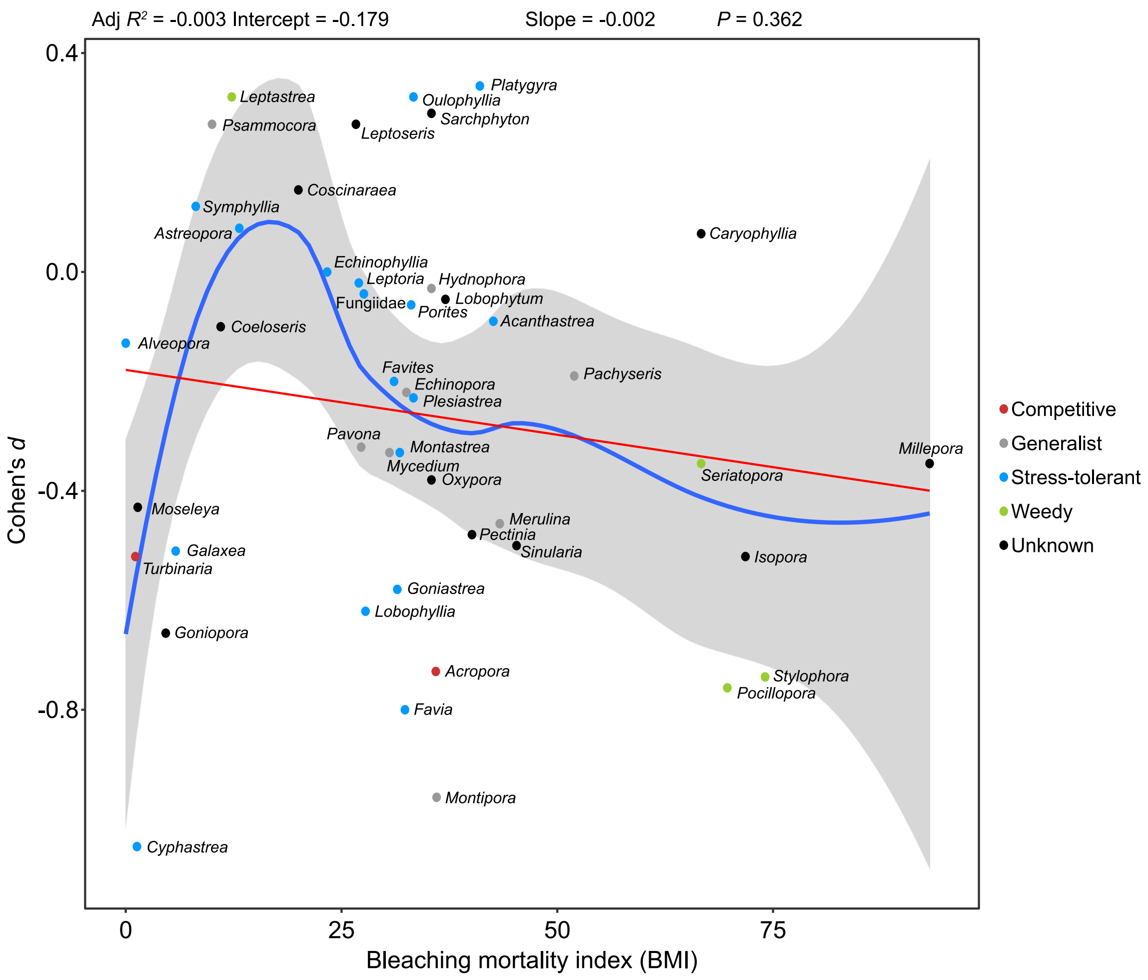

Fig. 8 Bleaching mortality index vs. effect size. Blue line represents the smooth line of LOESS smoother. Red line and the formula above represent the linear regression line and regression result. Colours indicate the ASG; competitive (red), generalist (grey), stress-tolerant (blue), weedy (green) and unknown (black)

abundance of stress-tolerant species in coral assemblage at higher latitudes (Sommer et al. 2014) in contrast to the predictions of UAST, i.e. that stress-tolerant species should dominate in unproductive habitats, such as these high latitude marginal reefs. This suggested either the current ASGs scheme used on reef corals (e.g. Darling et al. 2012) is inappropriate, or the UAST, developed from plants, is unsuitable for colonel creatures, such as reef corals.

In conclusion, ASGs rarely behaved as predicted in reef corals, which we attribute to marked response diversity within higher taxonomic groups and broadly defined adaptive groups. We suggest a direct trait-based approach (e.g. Mcwilliam et al. 2018) will be more informative to understand differential vulnerabilities of corals to changing disturbance regimes, and to predict potential shifts in species composition.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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