RAFFLES BULLETIN OF ZOOLOGY **65**: 525–538
Date of publication: 14 September 2017
http://zoobank.org/urn:lsid:zoobank.org:pub:933EEA83-D07E-49A3-9B64-ADBC3B773C00

Influence of a tropical marina on nearshore fish communities during a harmful algal bloom event

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Abstract. The influence of human-modified coasts on fish communities exposed to episodic environmental disturbance is poorly researched. To examine the influence of a tropical marina on nearshore ichthyofauna during a harmful algal bloom (HAB) event, we surveyed the fish communities within and outside Raffles Marina, Singapore, in a catch-and-release sampling program. Mean fish species richness, catch abundance, and diversity were higher within Raffles Marina before the HAB event. Immediately after the event, abundance and species richness of the fishes within the marina significantly decreased. Pre-HAB fish community index levels were attained six months after the event. No significant changes in community richness and abundance were observed outside the marina. Consistently, more fishes were caught within the marina than outside it. After one year, fish community structure within and outside Raffles Marina were significantly different when compared to pre-HAB levels. Our results suggest that Raffles Marina may mitigate local perturbations by providing shelter to fish communities. The need to understand how other artificial structures affect nearshore biota in light of increasingly frequent impacts is highlighted.

Key words. coastal development, environmental disturbance, marina, tropics

INTRODUCTION

Coastal development involves transformation of natural marine habitats into areas suitable for commercial, residential, and recreational purposes. The installation of artificial structures such as groynes, breakwaters, and pilings, protects these areas against strong wave action (Bulleri & Chapman, 2010). Such modifications however, have resulted in the unintended erosion of adjacent coastlines, degradation of local breeding and nursery grounds, alteration to marine community structure, natural habitat fragmentation, and overall reduction in biodiversity (Klein & Zviely, 2001; Bilkovic & Roggero, 2008; Walker et al., 2008; Peterson & Lowe, 2009; Bilkovic & Mitchell, 2013; Sundblad & Bergström, 2014). Yet, coastal modification projects continue unabated to cope with resource demands of an expanding global population (Dafforn et al., 2015). These development projects have precipitated investigations into the potential of modified coastal areas and associated structures to support and sustain marine organisms (Martin et al., 2005; Clynick, 2006; Pérez-Ruzafa et al., 2006; Chapman & Blockley, 2009; Bulleri & Chapman, 2010). Berthing pontoons, pilings, and seawalls in marinas, for instance, diminish flow rates and elevate levels of suspended sediment and metals, creating conditions vastly different from areas adjacent to, but outside, of these marinas (Rivero et al., 2013). The new conditions favour the recruitment of marine and estuarine species with short-lived larval stages (Rivero et al., 2013), and novel surfaces allow for the establishment of sessile faunal communities that may be uncommon in adjacent areas (Tan et al., 2012; Toh et al., 2016a). Consequently, these organisms function as food sources and shelter sites for other marine organisms (Rilov & Benayahu, 1998; Clynick et al., 2007; Toh et al., 2016b). The effects of structures such as marinas on coastal ichthyofaunal communities in the event of environmental disturbances (e.g., in cases of dystrophic crises and algal blooms; Koutsoubas et al., 2000; Ng et al., 2012), however, are not known.

Harmful algal blooms (HABs) are episodes of phytoplankton proliferation that can have debilitating impacts on aquatic ecosystems, ranging from light attenuation, to environmental anoxia and mass fish kills (Anderson et al., 2002; Landsberg, 2002). Although both natural (e.g., circulation, river flows, storms) and anthropogenic (e.g., eutrophication, ballast water discharge, overfishing) processes are known triggers of harmful algal growth (Heisler et al., 2008), the frequency and severity of their occurrences are exacerbated by the effects of a changing climate (Hallegraeff, 1993; Paul, 2008; Hallegraeff, 2010). The increase in incidences of ichthyotoxic algal blooms is raising concerns globally (Fu et al., 2012; Lee et al., 2013). In the last two decades alone, HAB events

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ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

resulted in significant losses to fisheries of up to US$18 million and US$60 million in the USA and South Korea respectively (Anderson et al., 2000; Park et al., 2013). In low energy environments such as modified and sheltered habitats, HAB events can recur during periods of drought when mixing is reduced and residence times are prolonged (Paerl et al., 2011; Paerl & Paul, 2012).

The frequency and severity of HAB events necessitate investigations into the cumulative ecological consequences to marine communities of modified coastlines. However, efforts are hampered by the dearth of baseline data from such areas within the tropics (Jaafar et al., 2004; Toh et al., 2016b). A prime example is Singapore, a small island nation within the Indo-west Pacific, whose coastline has been extensively altered to support industrial, residential and recreational sectors (Chou, 2006). Development and reclamation projects began in the 1960s and presently, more than 63% of the coastline comprises artificial structures such as seawalls (Lai et al., 2015). The coastal areas are also sites for container port facilities and seven marinas (Chou, 2008; Chou et al., 2010). Several algal bloom events have been recorded since 2009 within the Straits of Johor, an estuarine body of water between Singapore and Peninsular Malaysia (Fig. 1). Two of these incidences coincided with massive fish mortalities (Leong et al., 2015). The impacts of these HAB events have far-reaching implications as the Straits of Johor is used for capture fisheries and aquaculture. In February 2014, 39 fish farms located on the eastern and western sides of the strait lost approximately 160 tonnes of commercially valuable species including groupers, threadfin, and rabbitfish (Lee, 2014). At the same time, dead wild fishes were floating on the surface of the unusually reddish-brown waters of the strait, presenting symptoms of dermonecrosis. The impact was observed throughout the strait and extended to Raffles Marina, at the western tip of Singapore. Hundreds of surface-dwelling (e.g., *Toxotes* spp.), pelagic (e.g., *Monacanthus chinensis*, *Ellochelon vaigiensis*, *Etroplus suratensis*, *Siganus* spp., *Scatophagus argus*, *Pomacanthus annularis*), and demersal (e.g., *Plotosus* spp., *Arius* spp.) fish species were found dead (pers. obs.). Water samples collected adjacent to Raffles Marina harbored more than 120,000 cells ml^{-1} of *Takayama* sp. and *Karlodinium* sp., the likely species responsible for the mass fish kills (Leong et al., 2015).

Predicted escalations in algal bloom occurrences in modified coastal areas (e.g., Yang & Hodgkiss, 2004; Garcés & Camp, 2012) highlight the importance of investigating the influence of coastal infrastructures on the marine biota during such events. In this study, we examined the fish community within a marina before and after the occurrence of the February 2014 HAB event through a catch-and-release sampling programme. We aimed to: 1) establish if basal fish community composition were similar within and outside an equatorial marina, 2) compare the fish communities within and outside the marina immediately after an HAB event, and 3) examine differences between fish communities from the same monsoonal season in consecutive years. We hypothesised that the immediate impact of the February 2014 HAB event on nearshore fishes would be more severe within Raffles Marina, and that subsequently the fish communities both within and outside the marina would be different.

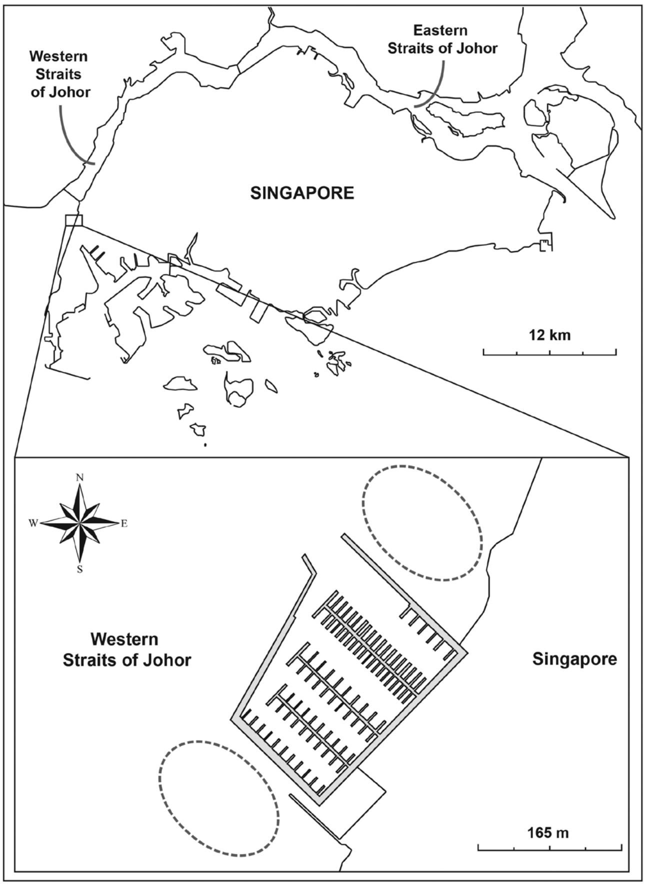

Fig. 1. Stylised maps of Singapore and Raffles Marina (inset). Dotted lines indicate areas outside Raffles Marina where fish traps were deployed.

MATERIAL & METHODS

Study sites. Raffles Marina (1°20′36.22″N, 103°′03.61″E) is at the western reach of the Straits of Johor. The marina is semi-enclosed, approximately 3.7 ha, and surrounded by vertical concrete walls with a single entry and exit point. Nearshore fishes were surveyed from December 2013 to January 2015 inside Raffles Marina ('within-marina'), and in areas up to 150 m beyond the marina within the western Straits of Johor ('outside-marina') (see Fig. 1).

Sampling regime. Fish traps were used to survey nearshore fishes due to the low visibility (<1 m) and high boat traffic at the study sites. From December 2013 to February 2014, a total of 18 and 15 replicate sets of traps were randomly deployed within and outside of the marina respectively. Three replicates were lost and/or damaged, and consequently, only 17 within-marina and 13 outside-marina sets were analysed. The data obtained from the period of December 2013 to February 2014 served as baseline levels of fish diversity. After the HAB event and ensuing mass fish kills in mid-February 2014, monthly surveys resumed from April 2014 to January 2015. Each month, six replicate sets of traps were each randomly deployed within and outside the marina. During this period, eight replicate sets were lost and/or damaged, thus a total of 53 within-marina and 48 outside-marina sets were analysed. One replicate comprised four customised fish traps made from thin galvanised steel wire (each measuring 0.6 m × 0.3 m × 1.0 m, with mesh size of 4.5 cm and a 20cm-wide entrance) and linked with ropes 3 m apart from each other. The traps were not baited. These were deployed onto the seabed and retrieved after three days. Each trapped fish was photographed and released at its catch site. Fishes were identified to the lowest possible taxonomic level following Allen et al. (2003) and Lim & Low (1998).

Statistical analyses. Adapting the temporal categories defined by Hajisamae and Chou (2003) for characterising fish communities in the eastern Straits of Johor, the data were pooled and analysed as seasons (i.e. three-monthly intervals): December 2013–February 2014 (DJF-13; i.e. pre-HAB, and baseline), March 2014–May 2014 (MAM-14; i.e. immediately after the HAB), June 2014–August 2014 (JJA-14), September 2014–November 2014 (SON-14), and December 2014–February 2015 (DJF-14). Our analyses indicated that monthly catch rates were not different within individual seasons (Supplementary Figs. 1, 2). As sampling was not completed in February 2014 and not conducted in March 2014 and February 2015, data from these months were not represented in DJF-13, MAM-14, and DJF-14 respectively.

Within- and outside-marina communities in DJF-13 (i.e. pre-HAB) were compared to investigate the influence of the marina on the nearshore fish communities. This data was also used as the baseline. Species richness (i.e. number of species caught per set of traps, S), catch abundance (i.e. number of fishes caught per set of traps, N), and species diversity (i.e. Shannon Wiener index per set of traps, H') were compared together using Hotelling's T^2 test (Johnson & Wichern, 2002). Simultaneous 95% confidence intervals for the difference in the indices were also computed to assess the marginal difference of each index. A principal coordinates analysis (PCoA) using Bray Curtis similarity and PERMANOVA was conducted using log-transformed data to establish if differences exist between fish communities within and outside the marina. Species that contributed highly to the difference in community were identified using SIMPER.

To examine the effect of the HAB event on the fish communities, catch abundance (N), species richness (S), and diversity (H') were simultaneously compared among seasons and between locations (i.e. within- and outside-marina) using a multivariate linear mixed model. Sampling month was added as a random effect to account for within-season variations. S and H' were square-root transformed to fulfill the assumptions of the linear model. The model was implemented in a Bayesian framework using the 'MCMCglmm' package in R (Hadfield, 2010). A factor was considered to have significantly contributed to the model if the p-value of one of its slope estimates was less than 0.05. The p-value here was interpreted as the proportion of time the estimate was less than 0 when the posterior mean was larger than 0 in the MCMC, or vice versa. With significant

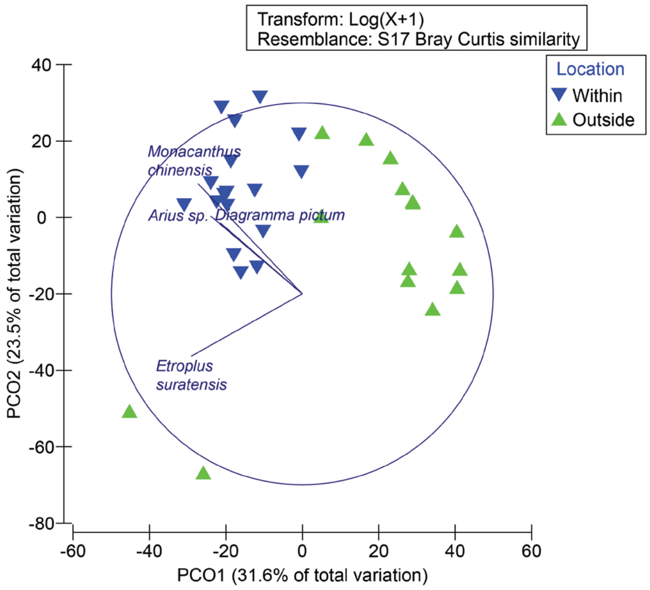

Fig. 2. Principal coordinates analysis of fish communities within and outside Raffles Marina before the harmful algal bloom event in February 2014. The two principal coordinates explained 55.1% of total variation. Factors shown within the circle correlate with PCO1 or PCO2 with a factor of at least 0.5.

interaction between seasons and locations, data from each combination of location and season were compared among each other, and p-value was adjusted using the false discovery rate method. The multiple comparison was conducted using the 'lsmeans' package in R.

To analyse seasonal changes in fish community at each location, principal coordinates analyses using Bray Curtis similarity and PERMANOVA were carried out. This was followed by pairwise comparisons between the seasons DJF-13, MAM-14 and DJF-14 to detect differences in fish community before the bloom (i.e. baseline), immediately after the bloom, and one year after the baseline (i.e. the same monsoonal season as the baseline but in the subsequent year). Species most responsible for the differences in data between these three seasons were identified by (a) overlaying vectors based on Spearman correlation between each species and each of PCO1 and PCO2, and (b) SIMPER analyses.

As the HAB event appeared to affect the within- vs outside-marina communities differently, we also conducted a beyond BACI analysis (Underwood, 1992). The outside-marina communities were divided into two groups: those north of the marina, and those south of it. Using three-factor ANOVA, the key metrics (N, S, H') of the within- and outside-marina communities were compared, as well as the communities north and south of the marina – the factors were (a) sampling period with respect to the HAB impact (i.e. before or after the HAB), (b) location (i.e. within-marina and outside-marina; north and south of marina), and (c) season (random factor nested within the sampling period). If there was an interaction between season and the within- and outside-marina communities (instead of with the north and south communities), the analysis would strongly support the finding that within-marina communities were more impacted. Additionally, the interaction of within- and outside-marina

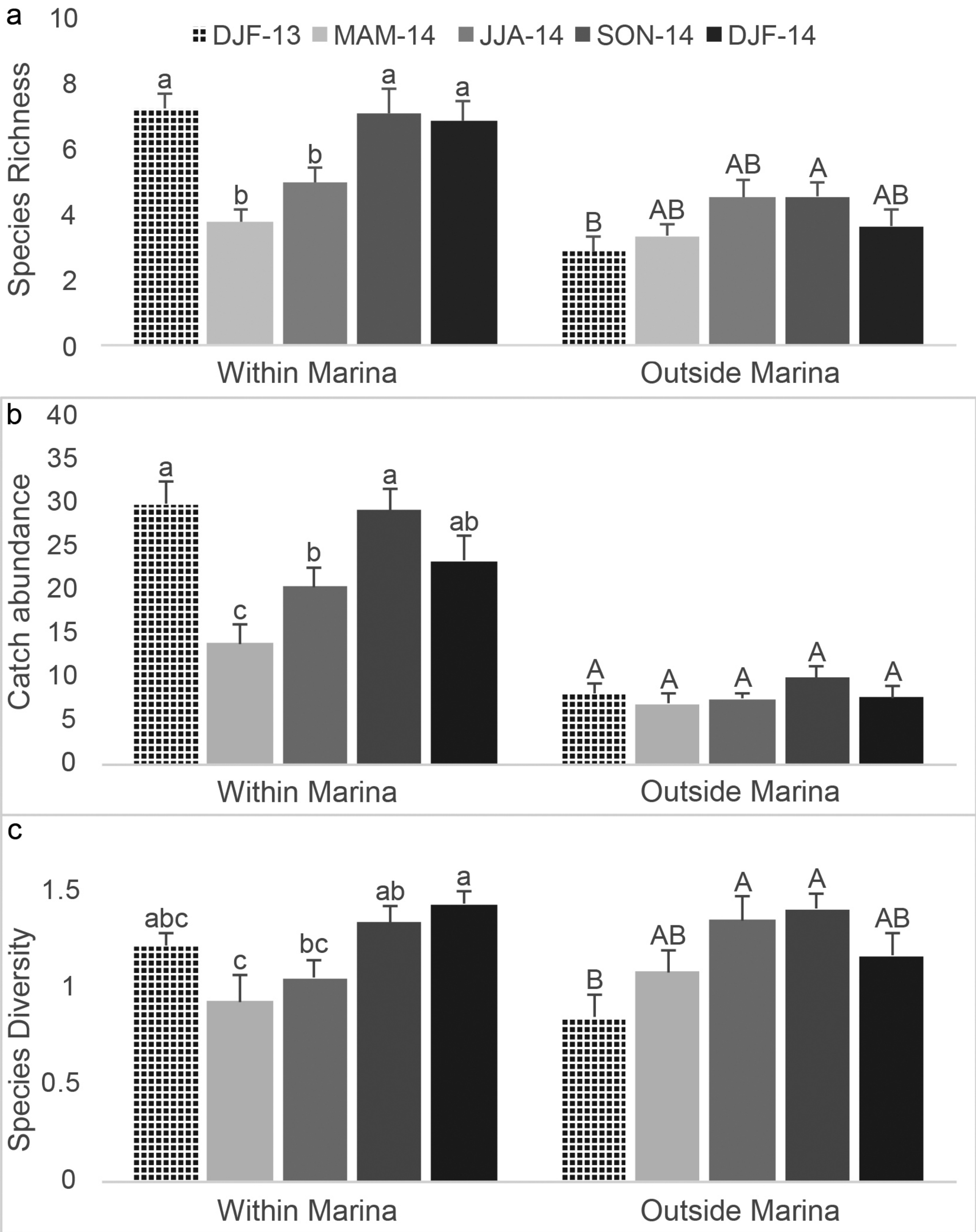

Fig. 3. Average a) Species richness, b) catch abundance, and c) species diversity (Shannon Wiener index) of fish communities within and outside Raffles Marina before and after a harmful algal bloom event in February 2014 (all means ± SE). DJF-13: December 2013–February 2014; MAM-14: March 2014–May 2014; JJA-14: June 2014–August 2014; SON-14: September 2014–November 2014; DJF-14: December 2014–February 2015. Seasons that are not significantly different are denoted by the same letter (lower case – within marina; upper case – outside marina).

Table 1. Overall species richness (S), catch abundance (N), and Shannon Weiner diversity index (H') of fish communities within and outside Raffles Marina, during the periods of pre-HAB (December 2013–January 2014), post-HAB (April 2014–January 2015), as well as when both periods are combined.

	Within Marina			Outside Marina		
	Pre-HAB	Post-HAB	Combined	Pre-HAB	Post-HAB	Combined
S	26	39	42	19	34	38
N	508	1329	1837	117	435	552
H'	1.64	1.88	1.87	1.55	2.55	2.45

communities with sampling period (i.e. before or after the HAB) would provide an indication of the differential effects of the HAB event. A similar analysis was also conducted on the macrobenthic community composition using three-factor PERMANOVA.

Hotelling's T^2 test, linear mixed model and ANOVA were implemented using R (R Core Team, 2016), while community analyses were carried out using PRIMER (v6.1.16; Clarke & Gorley, 2006).

RESULTS

General trends in nearshore fish communities. Within Raffles Marina, 508 and 1,329 fishes from 42 species (24 families) were recorded before (December 2013–January 2014; i.e. DJF-13) and after (April 2014–January 2015; i.e. MAM-14 – DJF-14) the algal bloom event respectively (Supplementary Tables 1, 2). The most abundant species within the marina were *Monacanthus chinensis* (56.1%), *Ostracion nasus* (10.6%), and *Plotosus lineatus* (5.1%). In the western Straits of Johor (i.e. outside Raffles Marina), 117 (pre-HAB) and 435 (post-HAB) fishes from 38 species (27 families) were recorded. The most abundant species outside the marina were *M. chinensis* (30.8%), *Scatophagus argus* (12.3%), and *P. lineatus* (7.1%). Overall species diversity was lower within (Shannon Weiner: $H'_{Within} = 1.87$) than outside the marina (Shannon Weiner: $H'_{Outside} = 2.45$) (Table 1). Species such as *M. chinensis* remained dominant within the marina regardless of the impact from the HAB event.

Fish community composition within and outside the marina. Fish communities within and outside the marina were significantly different prior to the HAB event (PERMANOVA: $F = 7.9$, $p < 0.001$) (Fig. 2). The mean species richness, catch abundance and diversity were substantially higher within-marina than outside-marina ($T^2 = 81.42$, $p < 0.001$, all confidence intervals did not contain zero; Fig. 3a, 3b). Dominant fishes within the marina were *M. chinensis* (62.8%), *Etroplus suratensis* (6.3%), *Siganus javus* (5.9%), *Sc. argus* (3.5%), and *Arius* sp. (3.3%). Outside the marina, *M. chinensis* (64.1%), *E. suratensis* (7.1%), and *Sc. argus* (6.8%) were most abundant.

Species that contributed highly to the 66.7% dissimilarity between fish communities within-marina and outside-marina were *M. chinensis*, *E. suratensis*, *Arius* sp., and *Si. javus*. All species were more abundant within the marina. In contrast, the community outside the marina had only 0.9% *Si. javus* and no *Arius* sp. Although *M. chinensis* and *E. suratensis* outside were proportionally higher than within, the absolute abundance of both species was less in the former location. Moreover, *E. suratensis* was recorded from only two out of all outside-marina traps (see Fig. 2); comparatively, this species was more evenly distributed for traps within the marina.

The overall average species richness and catch abundance within Raffles Marina was higher than those outside it for the entire duration of the study (i.e. pre- and post-HAB) despite significant interactions between location and season. However, average diversity did not differ between within-marina and outside-marina communities (discussed in detail below).

Effect of HAB event on within- and outside-marina fish communities. The HAB event affected the fish communities within and outside Raffles Marina differently. The multivariate linear mixed model showed significant effects of location ($p < 0.001$), season (p-value ranged 0.002–0.376) and interactions between the two factors (p-value ranged < 0.001–0.220) (Fig. 3). The random effect (month) was very small – its posterior mean variance was 0.0017 as compared to posterior residual mean variances that ranged from 0.1558 (diversity) to 0.8163 (abundance). The beyond BACI analysis also indicated that species richness and catch abundance within the marina exhibited temporal trends that were significantly different from the outside (Table 2), i.e. there were interactions between location and sampling period (i.e. before or after HAB). Between the communities outside the marina (i.e. north and south groups), no significant interaction was observed.

Species richness and catch abundance decreased drastically within the marina immediately after the HAB event (i.e. DJF-13: $S_{Within} = 7.2 \pm 0.5$, $N_{Within} = 29.9 \pm 2.5$; MAM-14: $S_{Within} = 3.8 \pm 0.4$, $N_{Within} = 13.8 \pm 2.1$) and remained significantly lower in MAM-14 and JJA-14. Subsequently, richness and abundance returned to pre-HAB levels in SON-14 ($S_{Within} = 7.1 \pm 0.7$; $N_{Within} = 29.1 \pm 2.4$), and DJF-14 ($S_{Within} = 6.8 \pm 0.6$; $N_{Within} = 23.4 \pm 2.8$). No significant changes were observed for catch abundance post-HAB outside the marina but species richness in SON-14 ($N_{Outside} = 4.5 \pm 0.4$) was significantly higher compared to DJF-13 ($N_{Outside} = 2.9 \pm 0.4$). Richness and abundance within the marina were higher than the outside in all seasons except for MAM-14, for which within- and outside-marina communities had similar values.

Table 2. Results of beyond BACI analysis on impacts of the 2014 harmful algal bloom event on macrobenthic richness, abundance, diversity (three-factor ANOVA) and community composition (three-factor PERMANOVA) at Raffles Marina.

Source of variation	df	Species Richness (S)			Abundance (N)			Diversity (H')			Community	
		MS	F		MS	F		MS	F		Pseudo-F	
Before vs After (B)	1	3.1057	0.7692		7.3379	9.2303	**	0.3339	6.1216	*	1.5129	
Season nested in B, T(B)	3	25.7677	6.3819	***	6.2721	7.8896	***	0.2294	4.2065	**	3.8394	***
Among Locations = L	2											
Within vs Outside (I)	1	164.8038	40.8172	***	142.4129	179.1406	***	0.2315	4.244	*	7.8834	*
Among Outside (O)	1	0.0004	0.0001		2.1443	2.6973		0.0107	0.1961		1.7764	
B x L	2											
B x I	1	45.1377	11.1793	**	4.1661	5.2406	*	0.721	13.2195	***	1.1578	
B x O	1	0.3335	0.0826		0.2684	0.3376		0.0003	0.0049		0.4926	
L x T(B)	6											
I x T(After)	3	12.9077	3.1969	*	2.0847	2.6223	+	0.0872	1.5979		2.6511	***
O x T(After)	3	1.2678	0.314		0.4517	0.5682		0.0421	0.7716		1.5471	+
Residuals	128	4.0376			0.795			0.0545			–	

* = p <0.05; ** = p < 0.01; *** = p < 0.001; + = 0.055> p > 0.05

Changes in species diversity were not apparent within and outside the marina. H' within the marina decreased slightly from DJF-13 to MAM-14 and then increased gradually to levels in DJF-14. However, diversity in DJF-13 (H'_{Within} = 1.21 ± 0.07) was not significantly different from MAM-14 (H'_{Within} = 0.92 ± 0.14) and DJF-14 (H'_{Within} = 1.43 ± 0.07). Outside the marina, diversity increased steadily from DJF-13 ($H'_{Outside}$ = 0.84 ± 0.12) to SON-14 ($H'_{Outside}$ = 1.40 ± 0.08), followed by a slight drop in DJF-14 ($H'_{Outside}$ = 1.16 ± 0.12). Only SON-14 and JJA-14 were significantly higher than DJF-13.

Temporal changes in macrobenthic composition were also significantly different between within- and outside-marina communities. This difference was more pronounced than between the outside-marina communities (beyond BACI analysis: Within vs Outside × Season, Pseudo-F = 2.65, $p < 0.001$; North vs South × Season, Pseudo-F = 1.55, $p \approx 0.05$; Table 2). Within the marina, the macrobenthic communities differed significantly among seasons over the study period (single-factor PERMANOVA: F = 5.94, $p < 0.001$) (Fig. 4); the community in DJF-13 was significantly different from that of MAM-14 (t = 2.79, $p < 0.001$), as well as DJF-14 (t = 2.40, $p < 0.001$); the communities within the latter two seasons also differed from each other (t = 2.58, $p < 0.001$). *Monacanthus chinensis* was the dominant species within Raffles Marina throughout the study period and contributed highly to the difference in fish community between all seasons (Table 3). While the average abundance of *M. chinensis* decreased in MAM-14, the species was proportionally similar to that in DJF-13 (~63%). However, in DJF-14, the proportion of *M. chinensis* reduced to 44.6%. Based on the SIMPER and PCoA analyses, the community in DJF-13 comprised a large proportion of *E. suratensis* and *Si. javus*, but this reduced immediately after the HAB event; *Arius* sp. and *Sc. argus* made up a larger proportion of the community in MAM-14. In DJF-14, *O. nasus* and *Parachaetodon ocellatus* dominated the fish community, while the proportions of *Arius* sp. and *Sc. argus* decreased to levels below that recorded in DJF-13.

Fish community outside Raffles Marina also differed significantly among seasons during the study (single-factor PERMANOVA: F = 2.69, $p < 0.001$) (Fig. 5). The differences in communities between DJF-13 and MAM-14 (t = 2.37, $p < 0.001$), and that between DJF-13 and DJF-14 (t = 1.46, p = 0.034) were significant, while that between MAM-14 and DJF-14 was not (t = 1.17, p = 0.24). Species contributing the most to the dissimilarity between seasons were *M. chinensis*, *Sc. argus*, *P. lineatus*, and *Lagocephalus lunaris*, with *M. chinensis* being the dominant species across the five seasons (Table 4). However, the average abundance of *M. chinensis* reduced immediately after the HAB event (from 18.8 in DJF-13 to 8.7 in MAM-14), and was lower than that in DJF-14 (10.3). In contrast, the abundance of *P. lineatus* and *Sc. argus* increased immediately after the HAB event; these fishes were more abundant in MAM-14 and in DJF-14, when compared to DJF-13. *Lagocephalus lunaris* was only recorded in MAM-14, accounting for 15.9% of the community composition.

Table 3. Average and percentage abundances of the six fish species that contributed most to dissimilarity within Raffles Marina in the seasons before, immediately after, and one year after the baseline, following a harmful algal bloom event in February 2014.

	Average Abundance			Percentage abundance		
Species	**DJF-13**	**MAM-14**	**DJF-14**	**DJF-13**	**MAM-14**	**DJF-14**
Arius sp.	1.0	1.3	0.3	3.4	9.1	1.5
Etroplus suratensis	1.9	0.0	0.2	6.3	0.0	0.7
Monacanthus chinensis	18.8	8.7	10.3	62.8	63.0	44.6
Parachaetodon ocellatus	0.7	0.0	2.2	2.4	0.0	9.4
Ostracion nasus	0.8	0.9	3.8	2.8	0.6	16.7
Scatophagus argus	1.1	1.7	0.4	3.5	12.1	1.8
Siganus javus	1.8	0.0	0.0	5.9	0.0	0.0

DJF-13: pre-HAB (baseline data); MAM-14: immediately after the HAB; DJF-14: one year after baseline.

Table 4. Average and percentage abundances of five fish species that contributed most to dissimilarity outside Raffles Marina in the seasons before, immediately after, and one year after the baseline, following a harmful algal bloom event in February 2014.

Species	Average Abundance			Percentage abundance		
	DJF-13	**MAM-14**	**DJF-14**	**DJF-13**	**MAM-14**	**DJF-14**
Lagocephalus lunaris	0.0	1.1	0.0	0.0	15.9	0.0
Monacanthus chinensis	5.0	2.5	3.1	64.1	36.6	41.7
Plotosus lineatus	0.3	0.9	0.9	3.4	13.4	11.7
Scatophagus argus	0.5	1.3	1.0	6.8	18.3	13.3

DJF-13: pre-HAB (baseline); MAM-14: immediately after the HAB; DJF-14: one year after baseline.

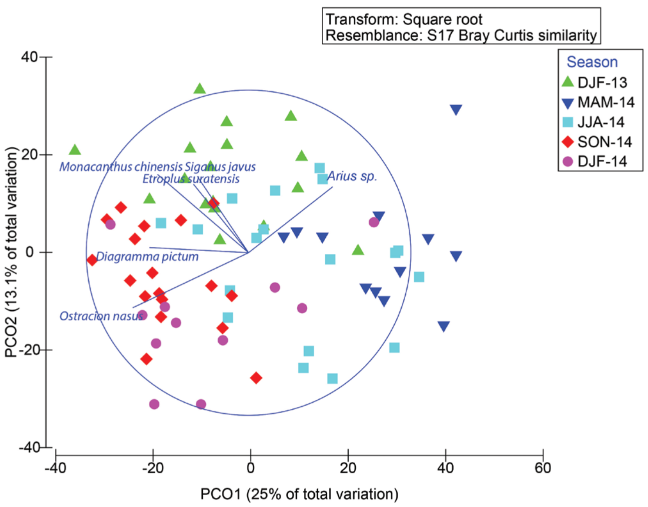

Fig. 4. Principal coordinates analysis of fish community within Raffles Marina before and after a HAB event in February 2014. The two principal coordinates explained 38.1% of total variation. Factors shown within the circle correlate with PCO1 or PCO2 with a factor of at least 0.5. (DJF-13: December 2013–February 2014; MAM-14: March 2014–May 2014; JJA-14: June 2014–August 2014; SON-14: September 2014–November 2014; DJF-14: December 2014–February 2015).

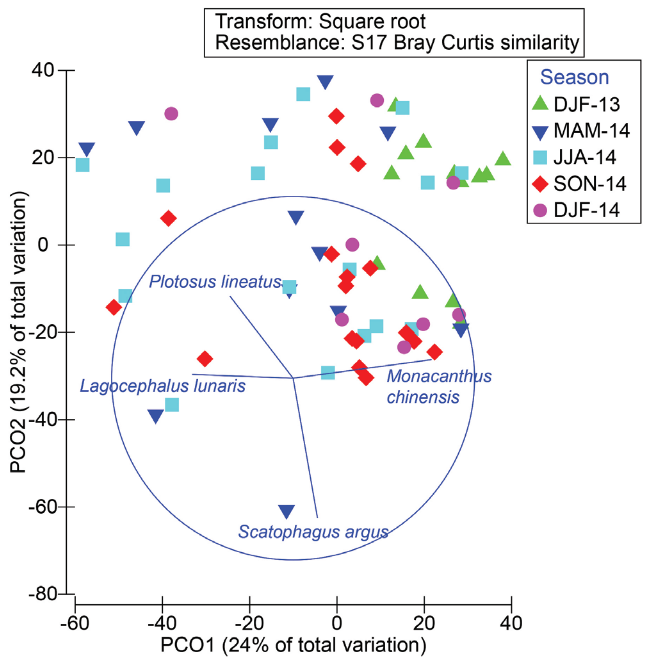

Fig. 5. Principal coordinates analysis of fish communities outside Raffles Marina before and after a harmful algal bloom event in February 2014. The two principal coordinates explained 43.2% of total variation. Factors shown within the circle correlate with PCO1 or PCO2 with a factor of at least 0.5. (DJF-13: December 2013–February 2014; MAM-14: March 2014–May 2014; JJA-14: June 2014–August 2014; SON-14: September 2014– ovember 2014; DJF-14: December 2014–February 2015).

DISCUSSION

Anthropogenic development is usually perceived as detrimental to the ecology of coastal zones. Although one marina and its surrounding environs were surveyed, our study highlights the possibility of highly modified marine environments supporting greater diversity and abundance of ichthyofauna compared to adjacent areas that are less modified. Raffles Marina is here shown to have a unique influence on nearshore fish communities during environmental perturbations in the Straits of Johor. Additionally, our findings offer timely insights on the complex phenomena of HABs and their effects on nearshore fishes in highly urbanised coasts.

The western Straits of Johor can support a high diversity of fishes in spite of anthropogenic activities and consequent impacts. Data from the pre-HAB event, here considered baseline information, suggest that artificial structures installed along the coast affected the distribution of ichthyofauna within the strait. The higher species richness, abundance, and diversity of fishes within the marina emphasised its role as a fish aggregator and/or attractor. The seabed of the western Straits of Johor lacks discernible organic and inorganic structures, and is characterised by silt-clay substrate (Wood et al., 1997). In contrast, pilings, pontoons and seawalls within Raffles Marina increased structural complexity throughout the water column and become novel substrates for colonisation. Marine epibionts attached and sheltered on these substrates and became prey items to other organisms (Clynick et al., 2007), thus jump-starting a novel community with niche specialisations (Jaafar et al., 2004).

Elsewhere, significant reductions in fish species richness, abundance and biomass followed HAB events (Gannon et al., 2009; Reis-Filho et al., 2012). Such effects are expected after an acute disturbance event, but the dissimilarity in the observed composition of fish communities within and outside Raffles Marina further underscores the differences between these adjacent locations. The impact of the HAB event was more pronounced within the marina, evident by the sharp decrease in catch abundance, richness and diversity of fishes in the immediate succeeding months. The semi-enclosed nature of the marina reduces water exchange and flushing, and likely exacerbated HAB-related impacts – a phenomenon often observed in low-energy environments such as harbours and estuaries (Garcés et al., 2006; Lim et al., 2014). In contrast, although the HAB event affected a wide stretch of the western Straits of Johor during a period of neap tide (Lim et al., 2014), there were insignificant differences in the abundance and species richness of fish communities between the pre-HAB and immediate post-HAB. Tidal influences in the comparatively larger expanse of the western Straits of Johor limited the impacts of the HAB on fish communities outside Raffles Marina.

The recoveries of marine fish populations following HAB events are not as extensively documented as the impacts themselves. As with our study, existing data based on freshwater fish communities indicate a similar recovery time of six months to return to pre-HAB event levels of abundance and species richness (Rhodes & Hubbs, 1992; Zamor et al., 2014). A steady colonisation of niches by individuals from outside Raffles Marina could have facilitated the recovery within the marina. The inflow of the young-of-the-year cohort between June and November 2014 could have similarly aided in the recovery, as we observed a greater percentage catch of smaller individuals of *M. chinensis* during this period. Incidentally, these months coincide with the reproductive seasons of numerous fish species that occur within Raffles Marina such as *P. lineatus* and *Diagramma pictum* (Grandcourt et al., 2011; Edelist et al., 2012). In contrast, the community outside the marina responded differently to the HAB event. The fish community abundance and richness reached pre-HAB event levels in less than three months, similar to the recovery pattern in estuarine fish assemblages in Brazil after a HAB event (Reis-Filho et al., 2012). The faster recovery duration demonstrates how large water bodies with high flushing rates can mitigate impacts of HAB events.

The surveys also revealed that fish community structures within and outside Raffles Marina had changed after the HAB event. Fewer fishes of all species were caught within the marina immediately after the HAB event (MAM-14) with the exception of *Arius* sp. and *Sc. argus*. Fish communities in the northeast monsoonal seasons of 2013 and 2014 (i.e. DJF-13 and DJF-14) were expected to exhibit minimal seasonal variation, but were significantly different, which was likely an effect of the HAB event. Before and immediately after the HAB event, *M. chinensis* remained proportionally the most abundant species within Raffles Marina, but its dominance later waned with the simultaneous three-fold rise in abundance of *Pa. ocellatus* and *O. nasus* in DJF-14. Outside the marina, the abundance of *M. chinensis* decreased immediately after the HAB event, and was accompanied by an increase in abundance of *P. lineatus*, *Sc. Argus*, and *La. lunaris*. The increase in *La. lunaris* in MAM-14 was likely tied to seasonal factors, as the species was absent in both DJF-13 and DJF-14. The same is unlikely for *P. lineatus* and *Sc. argus*; the abundances of both species had increased in MAM-14 and remained stable until DJF-14. The final percentage abundances of *P. lineatus* and *Sc. argus* were more than twice those of DJF-13, thus effectively reducing the dominance of *M. chinensis*. These observations provide clear evidence that HAB events have long-term implications for fish community structures both within and outside marinas.

Fish abundance and species richness returned to pre-HAB levels within six months both within and outside Raffles Marina, but diversity and community composition was altered. Post-HAB event shifts in community structure have also been reported elsewhere (e.g., Reis-Filho et al., 2012), but the permanence of such disturbances in marinas cannot be confirmed without long-term monitoring data and more study sites. The effects of the 2014 HAB event were more pronounced than regular seasonal variations of the fish communities. Even though the impacts from the HAB event were compounded by Raffles Marina's sheltered and low-flow environment, consistently more fishes were caught within than outside the marina regardless of season. These findings suggest that this marina could mitigate local and mid-level perturbations by acting as shelter for marine biotic communities.

Responses of marine communities to HAB events in anthropogenically-modified areas remain a poorly studied phenomenon despite the growing interest in their downstream impacts. The paucity of such information for tropical marine habitats restricts academic assessments on which management actions can be based. This trend is troubling especially because while these areas support high marine diversity, they are at the same time threatened by escalating urbanisation and coastal modification rates. As HAB events are often acute and cannot be replicated easily, any available information on the sort and scale of impacts should thus be reported and consolidated by scientists or coastal managers. In the current study, the localised nature of the HAB event meant that only one marina was affected, which seemingly limited comparisons that could be made on temporal and spatial scales. However, in light of increasingly frequent episodic disturbances, understanding the extent of influence of coastal infrastructure on nearshore biota has become even more important in order to develop sound mitigation and management strategies to further enhance the resiliency of marine ecosystems.

ACKNOWLEDGEMENTS

We thank Kelvin Lim, Tan Heok Hui and Jeffrey Low for assistance in fish identification. We are also grateful to the staff of Raffles Marina and members of the Reef Ecology Laboratory, NUS, for all help rendered over the course of this study. This study was funded and supported by the National Parks Board and the Technical Committee for the Coastal and Marine Environment (TCCME) (grant number R-154-000-557-490), and was carried out under permission by the Institutional Animal Care and Use Committee (IACUC), under application no. B13-5536, protocol no. 2013-05536.

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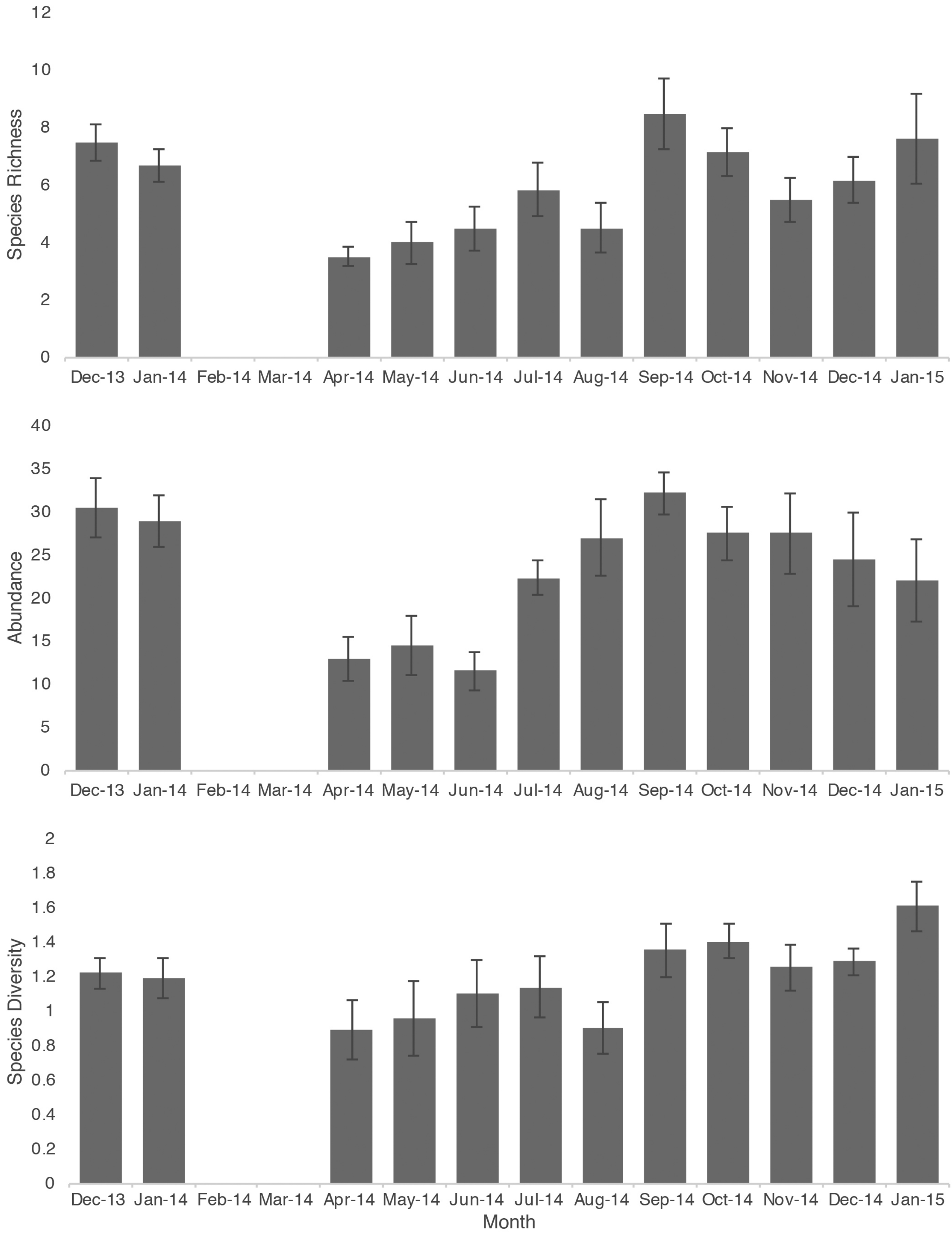
SUPPLEMENTARY INFORMATION

Supplementary Fig. 1. Monthly species richness, catch abundance, and species diversity (Shannon Wiener index) of fish communities within Raffles Marina before and after a harmful algal bloom event in February 2014 (all means ± SE). Sampling was not completed in February 2014 and not conducted in March 2014.

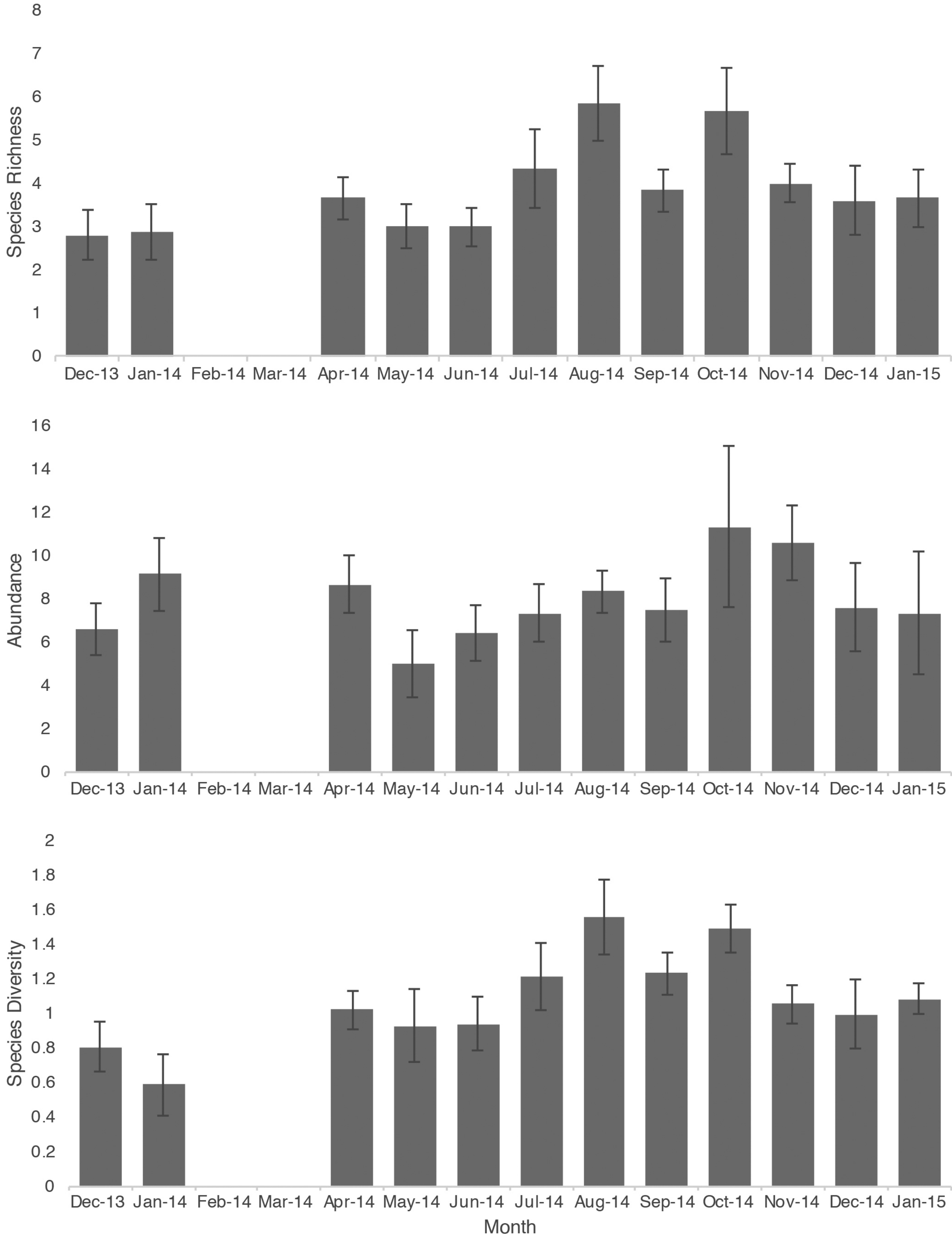


Supplementary Table 1. Fish species recorded within Raffles Marina from December 2013 to January 2015.

Family	Species	DJF-13	MAM-14	JJA-14	SON-14	DJF-14
Antennariidae	*Lophiocharon trisignatus*	×				
Ariidae	*Arius* sp.	×	×	×	×	×
Carangidae	*Carangoides praeustus*					×
	Caranx ignobilis				×	
	Selaroides leptolepis	×		×		
Chaetodontidae	*Chelmon rostratus*	×		×		
	Parachaetodon ocellatus	×			×	×
Cichlidae	*Etroplus suratensis*	×		×	×	×
Dasyatidae	*Himantura walga*		×			
	Taeniura lymma	×		×		
Ephippidae	*Platax* sp.				×	×
Gerreidae	*Gerres oyena*	×	×	×	×	×
Haemulidae	*Diagramma pictum*	×		×	×	×
	Plectorhinchus gibbosus			×	×	
	Pomadasys kaakan			×		
Labridae	*Choerodon oligacanthus*	×		×	×	×
Latidae	*Lates calcarifer*	×	×		×	
	Psammoperca waigiensis	×	×	×	×	×
Leiognathidae	*Gazza minuta*			×		
	Photopectoralis bindus				×	
Lethrinidae	*Lethrinus lentjan*				×	
Lutjanidae	*Lutjanus johnii*	×		×	×	×
	Lutjanus russellii			×	×	
Monacanthidae	*Acreichthys tomentosus*	×			×	
	Chaetodermis penicilligerus			×		
	Monacanthus chinensis	×	×	×	×	×
	Paramonacanthus choirocephalus			×	×	×
	Pseudomonacanthus macrurus	×				
Monodactylidae	*Monodactylus argenteus*					×
Mugilidae	*Ellochelon vaigiensis*					×
	Sp. 1	×				
Ostraciidae	*Ostracion nasus*	×	×	×	×	×
Plotosidae	*Paraplotosus albilabris*	×				×
	Plotosus canius	×	×	×	×	×
	Plotosus lineatus	×	×	×	×	×
Scatophagidae	*Scatophagus argus*	×	×	×	×	×
Sciaenidae	*Johnius belangerii*	×	×	×	×	
Serranidae	*Epinephelus coioides*	×	×		×	×
Siganidae	*Siganus guttatus*	×				×
	Siganus javus	×		×	×	
Tetraodontidae	*Lagocephalus lunaris*			×	×	
	Tetraodon nigroviridis			×	×	

DJF-13: December 2013–February 2014; MAM-14: March 2014–May 2014; JJA-14: June 2014–August 2014; SON-14: September 2014–November 2014; DJF-14: December 2014–February 2015.

Supplementary Fig. 2. Monthly species richness, catch abundance, and species diversity (Shannon Wiener index) of fish communities outside Raffles Marina before and after a harmful algal bloom event in February 2014 (all means ± SE). Sampling was not completed in February 2014 and not conducted in March 2014.



Supplementary Table 2. Fish species recorded outside Raffles Marina from December 2013 to January 2015.

Family	Species	DJF-13	MAM-14	JJA-14	SON-14	DJF-14
Apogonidae	*Ostorhinchus fasciatus*				×	
Ariidae	*Arius* sp.		×	×	×	
Batrachoididae	*Batrachomoeus trispinosus*	×	×	×		
Carangidae	*Carangoides praeustus*	×			×	×
	Caranx ignobilis	×			×	
Chaetodontidae	*Chelmon rostratus*	×			×	
	Parachaetodon ocellatus	×	×		×	×
Cichlidae	*Etroplus suratensis*	×		×	×	×
Dasyatidae	*Taeniura lymma*	×				
Ephippidae	*Platax* sp.					×
Gerreidae	*Gerres filamentosus*			×	×	
	Gerres oyena	×	×	×	×	×
Haemulidae	*Diagramma pictum*	×			×	×
	Plectorhinchus gibbosus	×				
	Pomadasys kaakan	×	×	×		
Labridae	*Choerodon oligacanthus*	×		×		
Latidae	*Psammoperca waigiensis*		×		×	
Leiognathidae	*Gazza minuta*			×		
Lethrinidae	*Lethrinus lentjan*			×		
Lutjanidae	*Lutjanus johnii*				×	×
	Lutjanus russellii			×	×	
Monacanthidae	*Monacanthus chinensis*	×	×	×	×	×
	Paramonacanthus choirocephalus			×		
Mugilidae	*Ellochelon vaigiensis*		×			×
	Sp. 1					×
Platycephalidae	*Cymbacephalus nematophthalmus*			×	×	
Plotosidae	*Paraplotosus albilabris*			×	×	
	Plotosus canius	×		×	×	
	Plotosus lineatus	×	×	×	×	×
Scatophagidae	*Scatophagus argus*	×	×	×	×	×
Sciaenidae	*Dendrophysa russelii*			×		
	Johnius belangerii		×	×	×	×
Scorpaenidae	*Pterois russelii*	×				
Serranidae	*Epinephelus coioides*		×	×	×	×
Siganidae	*Siganus javus*	×		×	×	×
Tetraodontidae	*Lagocephalus lunaris*		×	×	×	
	Tetraodon nigroviridis			×	×	
Triacanthidae	*Tripodichthys blochii*	×				

DJF-13: December 2013–February 2014; MAM-14: March 2014–May 2014; JJA-14: June 2014–August 2014; SON-14: September 2014–November 2014; DJF-14: December 2014–February 2015.