Bleaching susceptibility of aquarium corals collected across northern Australia

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Abstract There are a wide range of Scleractinian corals that are collected for the global reef aquarium market, often from non-reefal environments. The sustainability of coral harvesting is potentially threatened by increasing anthropogenic disturbances and climate change, though it is unknown to what extent many commonly harvested corals are susceptible to environmental change, or actually bleach during marine heatwaves. In this study, we experimentally tested the temperature sensitivity and bleaching susceptibility of six coral species (Homophyllia australis, Micromussa lordhowensis, Catalaphyllia jardinei, Trachyphyllia geoffroyi, Duncanopsammia axifuga, and Euphyllia glabrescens), which are important components of the aquarium coral fisheries across northern Australia, in Western Australia, the Northern Territory, and/or Queensland. Interspecific differences were evident in the temperature sensitivity and bleaching susceptibility among the study species. Homophyllia australis, and M. lordhowensis were found to be particularly susceptible to elevated temperatures, whereby all corals subjected to elevated temperatures died within the course of the experimental treatment (75 d). Catalaphyllia jardinei and E. glabrescens also exhibited significant increases in mortality when exposed to elevated temperatures, though some of the corals did survive, and C. jardinei mostly died only after exposure to elevated temperatures. The other species (T. geoffroyi and D. axifuga) exhibited marked bleaching when exposed to elevated temperatures, but mortality of these corals was similar to that of conspecifics held at ambient temperatures. This study highlights the potential for environmental change to impact the sustainability and viability of Australian coral harvest fisheries. More importantly, this study highlights the need for specific and targeted in situ monitoring for important stocks of coral fishery target species, to assess their vulnerability to fishery and fishery-independent effects.

Keywords Controlled experiment • Scleractinia • Temperature • Light intensity • Survivorship

Introduction

Mass coral bleaching is an increasingly familiar and recurring phenomenon, whereby many different species of zooxanthellate corals lose their endosymbionts and associated photosynthetic pigments (Glynn 1984), mainly in response to environmental stress, including freshwater inundation, aerial exposure, sedimentation and anomalous temperatures (Wiedenmann et al. 2013). The severity, extent and frequency of mass coral bleaching has increased since the 1980s (Hughes et al. 2018a) in line with ocean warming and increasing incidence of marine heatwaves (Heron et al. 2016; Hobday et al. 2018; Skirving et al.
2012). Marine heatwaves are now the foremost cause of mass coral bleaching and elevated coral mortality (Hughes et al. 2018a, b), threatening the population viability of vulnerable coral species and undermining the ecological integrity and function of reef ecosystems. Climate-induced coral bleaching, as well as other causes of coral mortality, may also directly undermine the sustainability and viability of harvest fisheries that collect corals from the wild, mainly for home and public aquaria (Harriott 2003; Rhyne et al. 2012).

International ornamental and aquarium coral fisheries involve the annual trade of hundreds of thousands of small coral pieces and are worth millions of dollars (Wood et al. 2012). An increasing portion of the coral sold comes from aquaculture; however the majority is still collected from the wild, from countries like Indonesia and the Philippines (Rhyne et al. 2012). In Australia, coral harvesting is a relatively minor cause of coral loss, and the annual biomass of coral removed is negligible compared to reef-wide levels of coral biomass and productivity (Harriott 2003). For the Queensland Coral Fishery (QCF) the annual Total Allowable Commercial Catch (TACC) is 200 tonnes, with fishing activity spread across a large area, and prohibited within no-take marine reserves (QDEEDI 2009). Reported catches have also been < 50% of the TACC throughout the last decade (DAF 2018). Coral fisheries in other jurisdictions (Western Australia, Northern Territory, and the Coral Sea) have much smaller quotas. Despite the limited overall harvesting, it is possible that specific species may be over-exploited where harvesting is concentrated on rare species. Aquarium corals are mostly selected based on appearance, especially colour, as well as their amenability to harvesting, transport and maintenance within aquaria. Few jurisdictions have species-specific quotas, and there is insufficient knowledge of wild stocks to even propose relevant harvest limits for most species (Roelofs and Silkock 2008). Aside from fisheries effects, widespread and accelerating degradation of coral reef ecosystems is placing increasing pressure on coral fisheries globally, leading to accelerating degradation of coral reef ecosystems is placing accelerating degradation of coral reef ecosystems is placing increasingly high pressure on coral fisheries globally, leading to greater public and political scrutiny regarding the sustainability of coral harvesting (Albert et al. 2015). The principal concern relates to the potential risk of localized depletion for vulnerable and slow-growing coral species (Harriott 2003; Garrabou et al. 2017). This concern is further magnified where harvested corals are simultaneously being impacted by fisheries-independent threats, including rapid and accelerating environmental change (Montero-Serra et al. 2019). Importantly, marine heatwaves have caused severe and widespread coral bleaching across Australia in recent years (Hughes et al. 2017), but it is largely unknown how these events impacted many of the corals (other than Acropora spp.) harvested by aquarium coral fisheries.

All zooxanthellate organisms are susceptible to temperature-induced bleaching at some level (Buddemeier and Fautin 1993), and very severe marine heatwaves can cause comprehensive bleaching and mortality across a wide range of different coral species (e.g., Vargas-Angel et al. 2019). There are however, apparent taxonomic differences in the susceptibility and responses of corals to increasing temperature (Loya et al. 2001; Grottoli et al. 2014; Hoey et al. 2016; Claar and Baum 2019). Among common, widespread and well-studied coral taxa, the rank order of bleaching susceptibility (based on the proportion of colonies that bleach or die) appears to be fairly conserved among geographic locations (e.g., McClanahan et al. 2004), whereby Acropora spp. are often the first to bleach and experience the highest mortality rates (Baird and Marshall 2002; Pratchett et al. 2013; Burt et al. 2019; but see Guest et al. 2012; Chou et al. 2016). Conversely, other corals, such as Turbinaria spp. are rarely observed to bleach (e.g., Marshall and Baird 2000) and appear particularly capable of withstanding thermal stress. There are many coral taxa for which we know very little about temperature sensitivity and bleaching susceptibility, mostly because they do not occur on shallow carbonate reefs, where in situ studies of coral bleaching are predominantly conducted (e.g., Hughes et al. 2017; Gilmour et al. 2019; Raymundo et al. 2019; but see Camp et al. 2018). This includes many of the coral taxa that are collected for the aquarium fishery from turbid intertidal habitats.

The purpose of this study was to assess the temperature sensitivity and bleaching susceptibility of six commonly harvested aquarium corals (Homophyllia australis, Micromussa lordhowensis, Catalaphyllia jardinei, Trachyphyllia geoffroyi, Duncanopsammia axifuga, and Euphyllia glabrescens), by exposing each of these coral species to elevated temperatures in aquaria. While such experimental studies are highly constrained in their capacity to assess how corals respond to elevated temperatures in the wild (Camp et al. 2018), there is a paucity of data regarding the bleaching susceptibility of these study species and experimental studies provide the most tractable way to assess relative bleaching susceptibility of poorly studied species.

Methods

Experimental set-up

This study was conducted in the Marine Aquarium Research Facility (MARFU) at James Cook University, in Townsville, Australia. Licensed coral collectors in Queensland (both CQ and NQ), WA and NT provided a total of 257 distinct corals (mostly whole colonies or individual polyps, but sometimes fragments) across 6
different study species (*H. australis, M. lordhowensis, C. jardinei, T. geoffroyi, D. axifuga, and E. glabrescens*) that were transported to Townsville within 1–2 weeks of collection. Where possible, samples of each coral species were obtained from Western Australia (WA), Northern Territory (NT), north Queensland (NQ) and central Queensland (CQ) (Table 1). All corals were mounted on ceramic discs, which were coded to distinguish individual corals and their provenance. Corals (1–2 individuals per species per location) were randomly assigned to each one of 12 different tanks across four different treatments (Fig. 1).

To test the bleaching responses and temperature sensitivity of the different corals, corals within the “heated treatments” were subject to gradual warming (1.0 °C change per week) until the temperature reached a maximum of 32 °C. The reason for using prolonged heating to relatively high maximum temperatures was intended to explicitly assess interspecific and regional variation in bleaching susceptibility, based on the time until individual corals exhibited bleaching. Temperatures in control tanks started at 25.6 °C and varied between 25.1 and 27.5 °C through the course of the experiment. Given most of the study species come from turbid inshore or deeper interreefal habitats, it was possible that bleaching susceptibility would be moderated by the light environment. To test this, we further divided corals into high and low light treatments, whereby the maximum light intensity (measured using a Li-Cor portable light meter during peak irradiance) was 208.0 (± 10.6 SE) and 48.7 (± 2.8 SE) μmol m⁻² · s⁻¹, respectively. These different light intensities are equivalent to those used to assess the role of light (> 180 μmol m⁻² · s⁻¹) in previous experimental bleaching studies (e.g., Wiedenmann et al. 2013), and are approximately equivalent to light regimes recorded in open reef environments versus shaded environments (e.g., within caves) at a depth of 5 m (Anthony and Hoegh-Guldberg 2003).

All colonies were acclimated to experimental conditions (ambient temperature and low light) for a minimum of 1-week before being subject to high light and/or experimental warming. The day that warming was initiated (April 9th 2018) was set as Day 1, and corals were subject to experimental conditions until Day 75, at which time experimental tanks with high temperatures were reduced to ambient temperatures over 72 h. We then continued to monitor all surviving colonies until Day 150. Corals were inspected every 1–2 d to record survival, and scored for colour, following Siebeck et al. (2006) every 1–2 weeks. Survival of individual coral colonies was recorded as the sum of the proportion of time a coral survived during the heating experiment plus the proportion of time the coral survived post treatment; i.e. corals that survived to day 75 (end of heating experiment) were assigned a survivorship of 1.0, and corals that survived to day 150 (end of study period) were assigned survivorship of 2.0. Changes in colour were based on changes in colour saturation (measured on a 6-point scale), between initial records taken on Day 1 versus Day 75 (or the last record of colour hue taken prior to mortality). Bleaching was defined as a change in colour saturation of 2 units or more, following Siebeck et al. (2006).

**Data analyses**

We modelled colour change and survival in corals as a function of ‘Temperature’ and ‘Light’ using linear mixed-effects models (Bates et al. 2015). ‘Species’, ‘Temperature’, and ‘Light’ were included as fixed effects. We also included the individual ‘Tank’ where the corals were placed as a random effect to account for the non-independence of replicates tested within the same aquarium. ‘Region’ was not included as a factor since some species were only sourced from one locality (see Table 1). Alternative models were compared using Akaike’s information criterion corrected for small sample sizes (AICc) following Burnham and Anderson (2002). Models were fitted using the ‘lmer’ function (library lme4) in R 3.0.1 (R Core Team 2019). Post hoc comparisons were conducted for survival data using the Tukey method in the R package emmeans (Lenth et al. 2018).

To better resolve differences in survival among corals, we obtained nonparametric estimates of the shape of the survivorship curves for each coral species under the two temperature treatments using Kaplan–Meier product-limit

| Species                  | NT | NQ | CQ | WA | Total |
|--------------------------|----|----|----|----|-------|
| **Family Lobophyllidae** |    |    |    |    |       |
| *Homophyllia australis*  | 17 | 17 |    |    | 34    |
| *Micromussa lordhowensis* | 18 | 18 |    |    | 36    |
| **Family Merulinidae**   |    |    |    |    |       |
| *Catalaphyllia jardinei* | 18 | 20 | 38 |    | 76    |
| *Trachyphyllia geoffroyi*| 18 | 23 | 15 | 56 | 102   |
| **Family Dendrophylliidae** |    |    |    |    |       |
| *Duncanopsammia axifuga* | 20 | 18 | 19 | 21 | 78    |
| **Family Euphyllidae**   |    |    |    |    |       |
| *Euphyllia glabrescens*  | 18 | 16 | 16 | 50 | 80    |
| **Total**                | 20 | 72 |113 | 52 |257    |

Source region: **NT** Northern Territory (Darwin), **NQ** North Queensland (Cairns), **CQ** Central Queensland (Mackay), **WA** Western Australia (Karratha). Corals were equally distributed among the four treatments.
|                | Ambient temp. Low light | Ambient temp. High light | Warming Low light | Warming High light |
|----------------|-------------------------|--------------------------|------------------|-------------------|
| *H. australis* | ![Image](image1)        | ![Image](image2)        | ![Image](image3) | ![Image](image4)   |
| *M. lordhowensis* | ![Image](image5)        | ![Image](image6)        | ![Image](image7) | ![Image](image8)   |
| *C. jardinei* | ![Image](image9)        | ![Image](image10)       | ![Image](image11) | ![Image](image12)  |
| *T. geoffroyi* | ![Image](image13)       | ![Image](image14)       | ![Image](image15) | ![Image](image16)  |
| *D. azya*     | ![Image](image17)       | ![Image](image18)       | ![Image](image19) | ![Image](image20)  |
| *E. glabrescens* | ![Image](image21)      | ![Image](image22)      | ![Image](image23) | ![Image](image24)  |
Results

Bleaching susceptibility

A total of 257 small (< 60 mm diameter) corals were used in the experiment (Table 1). Of these, 128 (49.8%) corals exhibited declines in colour saturation through the course of the experiment, with bleaching (where declines in colour saturation were > 2) recorded for 74 corals (28.8%). All six species exhibited bleaching (Fig. 2). The incidence of bleaching was consistently higher for corals subject to experimental warming (35.6%), though 16.67% of the bleaching was consistently higher for corals subject to warming versus ambient temperatures for H. australis (p = 0.028), and E. glabrescens (p = 0.001); but not for T. geoffroyi (p = 0.791) and D. axifuga (p = 0.270).

Survivorship

Eighty-five (out of 257; 33.1%) corals survived to the end of the experiment (150 d). Survivorship was lower (21.3%) among corals subject to warming, than for corals maintained at ambient temperatures (57.8%). However, there was also marked interspecific variation in the survival of corals between the two temperature treatments. The best model (based on wAICc) for explaining variation in survivorship included the interaction between ‘Species’ and ‘Temperature’, but did not include light levels (Table 2).

Post hoc pairwise comparisons showed that there were significant differences in survival between corals subject to warming versus ambient temperatures for H. australis (p < 0.001), M. lordhowensis (p < 0.001), C. jardinei (p = 0.028), and E. glabrescens (p < 0.001); but not for T. geoffroyi (p = 0.791) and D. axifuga (p = 0.270).

Survivorship of the different coral species varied both in extent and timing. For H. australis and M. lordhowensis, survival declined sharply from day 1 to day 75, during the treatment period for corals subject to warming (Fig. 4). Importantly, many colonies of H. australis died without exhibiting prior bleaching. For C. jardinei and E. glabrescens, there were also significant differences in survival with respect to temperature treatments, though this difference was most pronounced after the recovery period, on Day 150. For C. jardinei, differences in survival between temperature treatments were limited (92% vs. 81%) during the experiment, with bleaching (where declines in colour saturation were > 2) recorded for 74 corals (28.8%). All six species exhibited bleaching (Fig. 2).
the treatment period, from day 1 to day 75, but overall survivorship (at day 150) was much lower for corals subjected to warming (19%) compared to colonies maintained at ambient temperatures (75%) (Fig. 4c). There was

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*Fig. 2* Boxplots showing species-specific colour change response to temperature and light intensity treatments. Plots show median (bold line), 25th and 75th percentile range (box), 5th and 95th percentile range (error bars), and jitter points (large coloured circles) pooled across temperature treatments for each light treatment.
no difference in survival of *T. geoffroyi* or *D. axifuga* with respect to temperature treatments (Fig. 4). For *D. axifuga*, < 50% of corals survived 50 d, and there was ongoing mortality throughout the subsequent treatment and recovery period (Fig. 4e). Survival of *T. geoffroyi* was much higher than for *D. axifuga*, but there were sustained levels of mortality throughout the experiment both for corals exposed to elevated temperatures and those maintained at ambient temperatures (Fig. 4).

Based on standardised mean differences, elevated temperature had a substantial negative effect on the survival of *H. australis* (as well as for *M. lordhowensis*, which was excluded from analyses due to zero variance in the ‘Ambient’ treatment, i.e. 100% survival) and *E. glabrescens* (Fig. 3). Warming also had a moderate effect on the survival of *C. jardinei*, but we did not observe any adverse effect on *T. geoffroyi* and *D. axifuga*. For those species that did exhibit significant differences in survival between temperature treatments, interspecific differences in temperature sensitivity are also reflected in the time to median (50%) survival, which was lowest for *H. australis* (51 d), but also < 75 d for *M. lordhowensis* (58 d) and *E. glabrescens* (60 d), and longest for *C. jardinei* (118 d).

### Discussion

This study explored the temperature sensitivity and bleaching susceptibility of six different coral species (*H. australis, M. lordhowensis, C. jardinei, T. geoffroyi, D. axifuga, and E. glabrescens*), which are important target species for aquarium fisheries in QLD, WA and/or NT (DEEDI 2012; DPIR 2019; Newman et al. 2019). All six corals species exhibited bleaching to a greater or lesser extent under different light and temperature conditions.
Temperature: Ambient - Hot

(a) *Homophyllia australis*

(b) *Micromussa lordhowensis*

(c) *Catalaphyllia jardinei*

(d) *Trachyphyllia geoffroyi*

(e) *Duncanopsamnia axifuga*

(f) *Euphyllia glabrescens*

Survival Probability vs. Time (days)

- Homophyllia australis: \( p < 0.001 \)
- Micromussa lordhowensis: \( p < 0.001 \)
- Catalaphyllia jardinei: \( p = 0.003 \)
- Trachyphyllia geoffroyi: \( p = 0.560 \)
- Duncanopsamnia axifuga: \( p = 0.360 \)
- Euphyllia glabrescens: \( p < 0.001 \)
Most notably, *M. lordhowensis, C. jardinei, D. axifuga* and *T. Geoffroyi* exhibited significant colour loss (or bleaching) when exposed to elevated temperatures, and bleaching was exacerbated by high light intensity for *M. lordhowensis* and *D. axifuga*. Even more concerning however, were the high levels of coral mortality (> 80%) recorded for *H. australis, M. lordhowensis, E. glabrescens* and *C. jardinei* when these corals were subjected to elevated temperatures. Maximum temperatures to which corals were exposed in this experiment (32 °C) were high, though corals living in the shallow subtidal and intertidal zones in northern Australia may be exposed to temperatures ≥ 32 °C during severe heatwaves (Moore et al. 2012) or in areas where water pools for extended periods at low tide (Dandan et al. 2015).

While bleaching is commonly recorded among scleractinian corals exposed to elevated temperatures and/or high light intensity, there are marked interspecific differences in the responses of corals (Loya et al. 2001; Huerkamp et al. 2001; Dandan et al. 2015; Hughes et al. 2018b). In this study, *H. australis* was extremely sensitive to elevated temperature, whereby all colonies subjected to elevated temperatures had died within 60 d, even though this species rarely exhibited bleaching. Rather than losing colour, tissues of *H. australis* would retract in response to warming (Fig. 1) prior to complete mortality of the corals. Conversely, *T. Geoffroyi* exhibited a high incidence of bleaching when exposed to elevated temperatures, but low levels of mortality (< 50%). We observed yet another response for *C. jardinei*, for which, tissues would often detach from the underlying skeleton when subject to elevated temperature (Fig. 1). In many instances, the free-living tissue persisted ex situ and retained its colour intensity for the duration of the experiment. However, this is likely to be an experimental artefact, as free-living tissues of *C. jardinei* would likely be vulnerable to smothering or predation once dislodged in the wild. The only corals that exhibited more pronounced bleaching with increased light intensity were *M. lordhowensis* and *D. axifuga*, but this did not translate to differences in survivorship. Temperature and light act synergistically to influence bleaching susceptibility (Jokiel and Coles 1990), such that high turbidity in some nearshore environments may actually moderate bleaching-induced mortality during marine heatwaves (e.g., Fisher et al. 2019; Teixeira et al. 2019). However, this study shows that elevated temperatures are the predominant cause of bleaching and mortality, and the overriding concern for the corals considered in this study.

Interspecific differences in the environmental sensitivity and bleaching susceptibility among the six study species (*H. australis, M. lordhowensis, C. jardinei, T. Geoffroyi, D. Axifuga*, and *E. glabrescens*) may partially account for apparent differences in their abundance in different regions and habitats, or at least reflect the limited area over which corals were collected. Notably, the two coral species that were most susceptible to experimental warming (*H. australis* and *M. lordhowensis*) were provided exclusively from CQ, having been collected from the southern GBR in areas where these corals are relatively abundant. Both these corals are distributed further north on the GBR in much warmer waters (Veron et al. 2019), and it is possible that colonies from lower latitudes might exhibit greater resilience to elevated temperatures (sensu Hoegh-Guldberg 1999). Accordingly, *E. glabrescens* collected from WA exhibited much greater resilience to changing temperatures and light regimes, than conspecifics from the GBR. However, there was limited evidence of geographical variation in temperature sensitivity and bleaching susceptibility for *D. axifuga* (which was sampled from all four locations), nor for *T. Geoffroyi* (sampled from WA, NQ and CQ). Although, this experiment did not specifically account for local temperature regimes from where individual corals were collected (and then test bleaching susceptibility against regionally specific bleaching thresholds), we would have expected that corals provided from lower latitudes and warmer water in WA and NT would be more resistant to elevated temperatures than corals from CQ (sensu Hoegh-Guldberg 1999). Ultimately, it would be best to explicitly account for the specific environmental conditions in habitats from where each individual coral was collected, but this was not possible given that corals were provided by licenced coral collectors and their individual provenance was only broadly known.

This study shows that at least some Australian aquarium coral fishery target species (specifically, *H. australis, M. lordhowensis, E. glabrescens* and *C. jardinei*) are susceptible to elevated temperatures, thereby highlighting the potential for sustained and ongoing environmental change to undermine the sustainability and viability of these fisheries. More importantly, there is an increasing shift in aquarium coral collections and exports towards small polyp coral species (mainly, *Acropora* spp., Dee et al. 2014; Barton et al. 2017) which are, in general, even more susceptible to environmental change (Baird and Marshall 2002; Pratchett et al. 2013; Hughes et al. 2018b; Burt et al. 2019), though vulnerability assessments will need to be undertaken for the specific species that are targeted and habitats from which they are taken. Similarly, results for this preliminary experimental study should not be used to
infer relative or absolute vulnerability of the coral fishery target species to ocean warming, marine heatwaves, or changing environmental conditions. Rather, this study highlights the need for specific and targeted in situ monitoring for important stocks of coral fishery target species, to assess their vulnerability to fishery and fishery-independent effects.

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