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Corals in the hottest reefs in the world exhibit symbiont fidelity not flexibility

Running title: Symbiodiniaceae from the hottest reefs

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1 Abstract

2
3 Reef-building corals are at risk of extinction from ocean warming. While some corals can enhance
4 their thermal limits by associating with dinoflagellate photosymbionts of superior stress tolerance,
5 the extent to which symbiont communities will reorganise under increased warming pressure
6 remains unclear. Here we show that corals in the hottest reefs in the world in the Persian Gulf
7 maintain associations with the same symbionts across 1.5-years despite extreme seasonal warming
8 and acute heat stress ($\geq 35^{\circ}\text{C}$). Persian Gulf corals predominantly associated with *Cladocopium*
9 (clade C) and most also hosted *Symbiodinium* (clade A) and/or *Durusdinium* (clade D). This is in
10 contrast to the neighbouring and milder Oman Sea, where corals associated with *Durusdinium* and
11 only a minority hosted background levels of *Cladocopium*. During acute heat stress, the higher
12 prevalence of *Symbiodinium* and *Durusdinium* in bleached versus non-bleached Persian Gulf
13 corals indicates that genotypes of these background genera did not confer bleaching resistance.
14 Within symbiont genera, the majority of ITS2 rDNA type profiles were unique to their respective
15 coral species, confirming the existence of host-specific symbiont lineages. Notably, further
16 differentiation among Persian Gulf sites demonstrates that symbiont populations are either isolated
17 or specialised over 10s-100s of km. Thermal tolerance across coral species was associated with the
18 prevalence of a single ITS2 intragenomic sequence variant (C3gulf), definitive of the *C.*
19 *thermophilum* group. The abundance of C3gulf was highest in bleaching resistant corals and at
20 warmer sites, potentially indicating a specific symbiont genotype (or set of genotypes) that may
21 play a role in thermal tolerance that warrants further investigation. Together, our findings indicate
22 that co-evolution of host-Symbiodiniaceae partnerships favours fidelity rather than flexibility in
23 extreme environments and under future warming.

25 Introduction

26
27 The evolutionary success of coral reefs is underpinned by productive symbioses between
28 scleractinian corals and members of the Symbiodiniaceae, which grow the living foundation of
29 these ecosystems. Symbiodiniaceae are single-celled dinoflagellates that densely pack the
30 gastrodermis of coral hosts, providing an essential source of energy (nutritional photosynthates,
31 (Muscatine, Falkowski, Porter, & Dubinsky, 1984; Muscatine, McCloskey, & Marian, 1981;
32 Whitehead & Douglas, 2003) and enhancing skeletal growth rates (Cohen, Dubinsky, & Erez,

2016; Gattuso, Allemand, & Frankignoulle, 1999). However, anomalously warm temperatures can trigger a breakdown of this symbiosis (Weis, 2008), where corals become visually bleached from a loss of their pigmented symbionts and become starved of energy (Porter, Fitt, Spero, Rogers, & White, 1989). Depending on stress severity and duration, bleached corals suffer complete or partial mortality (e.g. Baird & Marshall, 2002), or may recover with suppressed growth (e.g. Goreau & Macfarlane, 1990; Suzuki et al., 2003), reproduction (e.g. Howells, Ketchum, et al., 2016; Szmant & Gassman, 1990; Ward, Harrison, & Hoegh-Guldberg, 2002), and/or disease resistance (e.g. Lewis, Neely, Richardson, & Rodriguez-Lanetty, 2017; Miller et al., 2009). Recent heat waves have caused major losses of coral cover from all ocean basins (Ateweberhan, McClanahan, Graham, & Sheppard, 2011; Eakin et al., 2010; Hughes, Kerry, et al., 2018), and the rapid rate of climate warming (up to $>3^{\circ}\text{C}$ above preindustrial by 2100, (Collins et al., 2013) threatens to outpace the capacity of corals to adapt (Hughes, Anderson, et al., 2018; Logan, Dunne, Eakin, & Donner, 2014).

Coral adaptation processes include genetic, epigenetic, and physiological responses in the coral host, Symbiodiniaceae partners, and associated microbes (reviewed in Barshis, 2015; Morrow, Muller, & Lesser, 2018; Quigley, Baker, Coffroth, Willis, & van Oppen, 2018; Torda et al., 2017). As bleaching is typically initiated by oxidative damage to Symbiodiniaceae and/or host cells (Oakley & Davy, 2018), any enhancements to the heat tolerance of Symbiodiniaceae partners is expected to confer bleaching resistance in the symbiosis. A diversity of Symbiodiniaceae taxa from at least four genera (*Symbiodinium*, *Breviolum*, *Cladocopium*, *Durisdinium*; formerly, *Symbiodinium* clades A-D; LaJeunesse et al., 2018) routinely associate with corals (reviewed in Coffroth & Santos, 2005). Heat tolerance varies widely among and within these genera (Swain, Chandler, Backman, & Marcelino, 2017; Tchernov et al., 2004), theoretically providing the opportunity for corals to replace sensitive symbionts with more tolerant taxa (Buddemeier & Fautin, 1993). Indeed, Symbiodiniaceae communities within coral colonies can undergo dynamic shifts in response to seasonal or acute temperature changes (Boulotte et al., 2016; Chen, Wang, Fang, & Yang, 2005; Jones, Berkelmans, van Oppen, Mieog, & Sinclair, 2008), with demonstrated increases to bleaching thresholds (Berkelmans & van Oppen, 2006; Jones et al., 2008; Silverstein, Cunning, & Baker, 2015). However, colonies of several coral species exhibit no changes in their Symbiodiniaceae communities during exposure to variable temperatures or bleaching stress (McGinley et al., 2012; Stat, Loh, LaJeunesse, Hoegh-Guldberg, & Carter, 2009; Thornhill,

LaJeunesse, Kemp, Fitt, & Schmidt, 2006). These contradictory observations have been linked to evolutionary differences among host and symbiont species in their capacity to associate with each other (Aranda et al., 2016; Putnam, 2012), inferior nutrition from novel symbionts (Cantin, van Oppen, Willis, Mieog, & Negri, 2009; Cunning, Silverstein, & Baker, 2015; Little, van Oppen, & Willis, 2004; Radecker et al., 2018), and the environmental availability of Symbiodiniaceae diversity (Cumbo, Baird, & Van Oppen, 2013; Cunning, Yost, Guarinello, Putnam, & Gates, 2015; Decelle et al., 2018). Alternatively, low taxonomic and quantitative resolution of early molecular identification approaches may have prevented the detection of fine-scale changes in Symbiodiniaceae communities (Boulotte et al., 2016; K. M. Quigley et al., 2014; Ziegler, Eguíluz, Duarte, & Voolstra, 2018), or the warming levels experienced by corals may not have been strong enough to drive community changes.

In this study, we investigated the dynamics of Symbiodiniaceae communities of reef-building corals in the northeastern Arabian Peninsula (Fig. 1). Corals in this region live in an extreme environment and can thus serve as a study system to understand the fate of coral-symbiont associations under future global warming scenarios. In particular, the southern Persian (Arabian) Gulf is home to the hottest coral ecosystems in the world, where daily average summer seawater temperatures are >34-35°C, and are lethal for corals elsewhere (Riegl, Purkis, Al-Cibahy, Abdel-Moati, & Hoegh-Guldberg, 2011). Gulf corals live exceptionally close to their upper thermal limits (Howells, Abrego, Meyer, Kirk, & Burt, 2016) and undergo repeated episodes of heat stress (Riegl et al., 2018). They also experience large shifts in temperature across seasons (~16°C) and hypersaline conditions (40-42 PSU; Bauman, Feary, Heron, Pratchett, & Burt, 2013). Variation in Symbiodiniaceae communities of common (*Cyphastrea microphthalma* and *Platygyra daedalea*) and rare (*Acropora downingi*) corals was quantified by high-resolution next-generation sequencing and profiling of the ITS2 rDNA marker (Hume et al., 2019). Communities were tracked in individual coral colonies for up to 1.5 years encompassing seasonal temperature changes and a coral bleaching event. We evaluated the effects of host identity, site, season, and bleaching severity on the community composition of Symbiodiniaceae genera, ITS2 type profiles, and sequences.

97 **Materials and Methods**

98

99 **Collection of coral samples**

100

101 We characterised the community composition of endosymbiotic dinoflagellates (Family
102 Symbiodiniaceae) in reef-building corals that acquire their symbionts from the Persian Gulf and
103 Oman Sea environments. Individual colonies of *Acropora downingi* ($n = 25$), *Cyphastrea*
104 *microphthalma* ($n = 53$), and *Platygyra daedalea* ($n = 50$) were tagged at Delma (24.5208°N,
105 52.2781°E), Saadiyat (24.5986°N, 54.4201°E), Ras Ghanada (24.8482°N, 54.6903°E), Dibba
106 (25.6031°N, 56.3485°E), and Al Aqah (25.4929°N, 56.3635°E; Fig. 1a). These five sites were
107 located at 4-7m depth and separated by 13-580 km (Fig. 1a). Within sites, colonies were located
108 along transects at uniform depth (<1m variation) and temperatures were recorded using loggers
109 attached to the reef substrate (HOBO pendant or TidbiT v2) (Fig. 1b). For each colony, 1-2cm² of
110 tissue from the upper central section was collected and preserved in 100% ethanol and
111 photographs were taken to provide visual health records.

112

113 All 128 colonies were first sampled in September 2012, at the end of an anomalously hot summer
114 in the Persian Gulf where water temperatures exceeded 35°C (Fig. 1b). At two of the study sites
115 (Saadiyat and Ras Ghanada) widespread coral bleaching was observed (see (Howells, Ketchum, et
116 al., 2016; Shuail et al., 2016), providing an opportunity to investigate the effect of bleaching
117 severity on Symbiodiniaceae community composition. Individual colonies were visually scored as
118 healthy (dark/normal pigmentation), moderately bleached (pale pigmentation), or severely
119 bleached (white pigmentation). In the aftermath of the bleaching, many *A. downingi* colonies died,
120 whereas all tagged colonies of *C. microphthalma* and *P. daedalea* survived. In recovering
121 colonies, egg numbers in the reproductive season following the bleaching event were quantified as
122 described in Howells, Ketchum, et al. (2016). This enabled us to evaluate whether
123 Symbiodiniaceae community composition during bleaching was associated with variation in the
124 reproductive output of surviving colonies. Subsets of the tagged colonies were resampled in April
125 2013 ($n = 116$), September 2013 ($n = 67$), and February 2014 ($n = 61$). Combined with the initial
126 samples, this schedule followed the warmest and coolest months over two consecutive years,
127 which spanned annual ranges of 16°C for the Persian Gulf sites and 10-11°C for the Oman Sea

sites (Fig. 1b). This allowed us to detect any changes in Symbiodiniaceae communities associated with large seasonal changes in temperature.

Next-generation sequencing of Symbiodiniaceae endosymbionts

For each sample, a few mm³ of preserved tissue/skeleton were transferred to 750 µl of DNA extraction buffer (100 mM Tris/EDTA/NaCl, 1% SDS) and incubated overnight at 65 °C. Proteins were removed from chilled extracts (1 M potassium acetate), and DNA was precipitated (100% isopropanol), washed (70% ethanol), re-suspended (0.1 M Tris), and stored at 4 °C. PCR amplifications of the Symbiodiniaceae ITS2 rDNA region were performed following (Arif et al., 2014). The primers ITSintfor2 and ITS2-reverse (LaJeunesse, 2002) were used with adapters (underlined) for sequencing on the Illumina MiSeq platform: 5'-

TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGGAATTGCAGAACTCCGTG-3'

(MiSeq-ITSintfor2) and 5'-

GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGGGGATCCATATGCTTAAGTTCAG

CGGGT-3' (MiSeq-ITS2-reverse). Triplicate 25 µl reactions were performed in Qiagen Multiplex

Master Mix (Qiagen) and 0.1 µM under the following conditions: 94°C (5 min); 27 cycles of 94

°C (30 sec) 51°C (30 sec), 72°C (30 sec); 72 °C (10 min). Amplification was verified by

visualisation on 1% agarose gels. Triplicate PCRs of each sample were pooled and cleaned with

the Agencourt AMPure XP magnetic bead system (Beckman Coulter). Nextera XT indexing and

sequencing adapters were added via PCR (8 cycles) following the manufacturer's instructions.

Sample libraries were quantified on the BioAnalyzer (Agilent Technologies) and QuBit (Quant-IT

dsDNA Broad Range Assay Kit; Invitrogen) and pooled in equimolar ratios. This pool of libraries

was purified on a 2 % Agarose gel to remove any excess primer and sequenced at 8pM with 10 %

phiX on the Illumina MiSeq, 2 x 300bp paired end version 3 chemistry according to manufacturer

specifications. Sequence data determined are available under NCBI BioProject ID PRJNA532516.

Identification of Symbiodiniaceae genetic diversity

Raw sequences for each sample (i.e., pairs of demultiplexed fastq.gz files) were processed using

the SymPortal analytical framework (symportal.org) which is described in detail in (Hume et al.,

2019). Sequencing information was submitted to the SymPortal remote database and underwent

quality control including the removal of artefact and non-Symbiodiniaceae sequences. Following quality control, each of our samples were represented by an average of 16,000 ITS2 rDNA sequences (range: 2,000-47,000). Symbiodiniaceae genera (formerly *Symbiodinium* clades; see LaJeunesse et al., 2018) were identified as part of the SymPortal analysis through blast querying a database containing representatives of each genus. Sub-generic ITS2 type profiles were designated by SymPortal based on the presence and abundance of the ITS2 sequences in our samples and within the SymPortal database. In brief, sets of sequences found to re-occur in multiple samples were searched for algorithmically. This search operates on a principle whereby the probability that a given set of ITS2 sequences found in a single coral sample is representative of a single Symbiodiniaceae genotype increases with the number of samples that set of sequences is found in. In this way, SymPortal differentiates between intra- and intergenomic sequence diversity within samples. The individual sequences (referred to as ‘defining intragenomic [sequence] variants’; DIVs) making up these re-occurring sets were used to define the ITS2 type profiles. Genera and type profiles at <1% proportional abundance within samples were excluded from downstream analyses.

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177 **Data analysis**

178

Symbiodiniaceae genera were initially analysed using the complete dataset evaluating host species, region, and season as potential drivers of symbiont community composition. These variables were analysed as crossed factors in a permutational multivariate analysis of variance (PERMANOVA) with colony included as a nested factor within the host species by region interaction. The model was performed using the *vegan* package in *R* (*vegdist* and *adonis* functions; Oksanen et al., 2019) with Bray-Curtis dissimilarities of proportional abundance data which were square-root transformed to increase the representation of rare taxa. Where significant model terms contained more than two groups, subsequent pairwise tests were performed and *P* values were adjusted for multiple comparisons (false discovery rate procedure; *pairwise.adonis* wrapper function; Martinez Arbizu, 2017). An additional PERMANOVA was performed on the Persian Gulf data using the same model features as above to investigate variation in Symbiodiniaceae genera among specific sites and time-points for *C. microphthalma* and *P. daedalea*. However, *Acropora downingi* data were excluded due to low replication across factors. The effect of coral

bleaching on Symbiodiniaceae associations was evaluated by comparing the prevalence of non-dominant genera in bleached versus non-bleached colonies, relative to the dominant *Cladocopium* (clade C). One-sample t-tests for the prevalence of *Symbiodinium* (clade A:C ratio) and *Durusdinium* (clade D:C ratio) in bleached corals were performed against mean values for unbleached colonies due to zero or near-zero variances in the latter group (*t.test* function). Data were pooled across coral species (*C. microphthalma* and *P. daedalea*) and sites (Saadiyat and Ras Ghanada), as the levels of these factors did not differ from one another during the bleaching event. Symbiodiniaceae composition in bleached corals was further investigated to see whether there was any relationship between the abundance of non-dominant Symbiodiniaceae genera and reproductive output during bleaching recovery. Oogenesis in *C. microphthalma* and *P. daedalea* commenced during or shortly after the bleaching event in September 2012 (see A. Bauman, Baird, & Cavalcante, 2011) and mature eggs were counted in samples collected in April 2013 (Howells, Ketchum, et al., 2016). Correlation between the abundance of *Symbiodinium* + *Durusdinium* (clade A + D) and the number of eggs per polyp mesentery was tested separately for *C. microphthalma* and *P. daedalea* (*cor.test* function).

Symbiodiniaceae ITS2 type profiles classified by SymPortal were analysed separately for *Cladocopium* (C, *n* = 23 ITS2 type profiles) and *Durusdinium* (D, *n* = 12 ITS2 type profiles). To verify ecological patterns observed among ITS2 type profiles, analyses were also performed on the underlying ITS2 sequences in which proportional abundance was $\geq 1\%$ within samples (C, *n* = 32 sequences; D, *n* = 19 sequences). No further analysis was undertaken of *Symbiodinium* (clade A) which comprised only one unique ITS2 sequence at $\geq 1\%$ abundance. PERMANOVAs were performed on Bray-Curtis dissimilarities of square-root transformed data, as outlined above. Initial models showed that there were no temporal effects on type profiles or sequences for either Symbiodiniaceae genus. Consequently, subsequent models only included samples from the first time-point in which all colonies were represented. *Cladocopium* analyses tested host species and site as crossed factors across all colonies from the Persian Gulf. *C. microphthalma* colonies hosting *Cladocopium* in the Oman Sea were also included in analyses. However, due to lack of replication, a single *A. downingi* colony from Saadiyat and a single *P. daedalea* colony from the Oman Sea were excluded. The effect of coral bleaching on *Cladocopium* associations was tested separately for each host species (*C. microphthalma* and *P. daedalea*) with site (Saadiyat and Ras Ghanada) included as a model factor comparing associations in bleached versus non-bleached

colonies. Additionally, the association between coral bleaching and the abundance of the C3gulf ITS2 sequence variant of *Cladocopium* was evaluated with a two-sample t-test and accompanying effect sizes (Cohen's *D*) were calculated with the *lsr* package (*cohensD* function; Navarro, 2015). *Durusdinium* analyses tested host species as a main factor across all colonies from the Oman Sea. For *A. downingi*, host effects are confounded with site, as colonies were collected from a nearby distinct site (Dibba) 13 km away from *C. microphthalma* and *P. daedalea* (Al Aqah). Due to the limited spread of *Durusdinium* across host species and sites in the Persian Gulf, samples from this region were excluded. Variation among *Cladocopium* sequences from the Persian Gulf and *Durusdinium* sequences from the Oman Sea were visualised using principal coordinates analyses of the dissimilarity matrices using the *ape* package (*pcoa* function; Paradis, Claude, & Strimmer, 2019).

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241 Results

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243 Symbiodiniaceae genera

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Associations with Symbiodiniaceae genera in the corals *Acropora downingi*, *Cyphastrea microphthalma*, and *Platygyra daedalea* were most strongly affected by the region of origin ($R^2 = 0.92$, Table S2, Supporting Information). Colonies from the thermally extreme Persian Gulf were dominated by *Cladocopium* (clade C, 99%, $n = 273$), while those from the milder Oman Sea were dominated by *Durusdinium* (clade D, 100%, $n = 99$) (Fig. 2). Sequences belonging to additional genera were detected in all colonies from each region during at least one sampling season (i.e. 94% of genotyped samples, $n = 372$), but were usually at very low abundances ($<0.1\%$). Once an abundance threshold of 1% was applied, associations with multiple genera were retained in the majority of Persian Gulf colonies (66%, $n = 94$), but only a minority of Oman Sea colonies (24%, $n = 34$). In the Persian Gulf, *Cladocopium* often co-occurred with low levels of *Symbiodinium* (clade A) and/or *Durusdinium* in both *C. microphthalma* (78% of colonies) and *P. daedalea*

256 (66%), and occasionally with *Durusdinium* in *A. downingi* (33%) (Fig. 2). In the Oman Sea,
257 *Durusdinium* associations were sometimes accompanied by *Cladocopium* in *C. microphthalmum*
258 (58% of colonies), but additional symbiont genera were virtually absent in the other host species.

259

260 The higher diversity of Symbiodiniaceae genera in the Persian Gulf corals did not correspond with
261 sampling season. Despite exposure to extreme seasonal changes in temperature ($\Delta 16^\circ\text{C}$), no
262 consistent shifts were observed in the composition of symbiont genera in coral colonies (Fig. 2;
263 Table S2). The only significant seasonal effect was for *C. microphthalmum* at Delma, where
264 *Symbiodinium* was detected (in two colonies) during only the first time-point. Additionally, no
265 seasonal effects were detected over smaller temperature changes ($\leq 11^\circ\text{C}$) in the Oman Sea
266 (PERMANOVA, pseudo- $F_{3,98} = 0.31$, $P > 0.05$). However, during the heatwave in 2012, there was
267 higher prevalence of *Symbiodinium* within bleached versus non-bleached colonies (Wilcoxon test, W
268 $= 228$, $P = 0.04$); as well as a non-significant tendency for higher levels of *Durusdinium* ($P >$
269 0.05). Either or both of these genera were present within most bleached colonies of *C.*
270 *microphthalmum* (61%, $n = 23$) and *P. daedalea* (61%, $n = 23$), where *Symbiodinium* levels reached
271 up to 54% (mean = 9%) and *Durusdinium* levels were up to 11% (mean = 2%) (Fig. 2). In
272 contrast, among the few colonies which resisted bleaching ($Cm = 6$; $Pd = 1$), none hosted
273 *Symbiodinium* and only two hosted low levels ($<4\%$) of *Durusdinium*. In the aftermath of
274 bleaching, the reproductive output of *P. daedalea* colonies declined (Howells, Ketchum, et al.,
275 2016) and was also weakly correlated with the composition of symbiont genera ($R = -0.37$, $P_{\text{one-}}$
276 $\text{tailed} = 0.047$; Fig. S1a). Egg numbers varied widely among bleached *P. daedalea* colonies that only
277 hosted *Cladocopium* around the onset of gametogenesis (Bauman et al. 2011), but declined in
278 colonies with a higher prevalence of *Symbiodinium* and *Durusdinium*. For *C. microphthalmum*,
279 reproductive output was unaffected by bleaching (Howells, Ketchum, et al., 2016) or the
280 prevalence of symbiont genera (Fig. S1b).

281

282 Symbiodiniaceae ITS2 type profiles and sequence composition

283

284 Associations with the ITS2 type profiles identified by SymPortal (<http://symportal.org/>) were
285 highly structured by host species and site of origin (Table S3). In the *Cladocopium* (clade C)
286 dominated associations of the Persian Gulf, almost all type profiles (17 of 19, 89%) were only
287 found in single host species (*A. downingi* = 3 of 4, *C. microphthalma* = 7 of 9, *P. daedalea* = 7 of
288 8) (Fig. 3; Table S3). These specific type profiles were also unique to individual sites (14 of 17,
289 82%) or two neighbouring sites (3 of 17, 18%). Although *Cladocopium* was not dominant in the
290 Oman Sea, associations with *C. microphthalma* in this region were also comprised of type profiles
291 that were both host and site-specific (Fig. S3). Similarly, in the *Durusdinium* (clade D) dominated
292 associations of the Oman Sea, all type profiles (8 of 8, 100%) were unique to a single host species:
293 *A. downingi* (3), *C. microphthalma* (3), or *P. daedalea* (2) (Fig. 4). In contrast, in the background
294 associations in the Persian Gulf (Fig. S4), most *Durusdinium* type profiles were shared among host
295 species (7 of 10, 70%) and sites (6 of 10, 60%), and a single *Symbiodinium* (clade A) type profile
296 was shared among host species and sites.

297

298 The ITS2 rDNA sequences underlying SymPortal type profile classifications confirmed the
299 observed pattern of associations that were highly structured by host species and site (Fig. 5; Table
300 S4). Our dataset comprised numerous sequences ($\geq 1\%$ abundance) belonging to *Cladocopium*
301 (32), *Durusdinium* (19), and *Symbiodinium* (1). ITS2 type profiles from within the same genus
302 (*Cladocopium*, *Durusdinium*) shared common major sequences and were distinguished by the
303 presence and identity of additional major (the most abundant defining intragenomic variants,
304 DIVs, of the type profiles found) and minor sequences (non-major DIVs; Table S1). Within
305 *Cladocopium*, C3 was the major sequence shared by the Persian Gulf type profiles in all host
306 species, while C15 was dominant in the Oman Sea type profiles in *C. microphthalma*. Consistent
307 with the SymPortal type profile classifications, 26 (81%) of the minor *Cladocopium* ITS2
308 sequences were unique to individual host species (*A. downingi* = 1 of 4, *C. microphthalma* = 15 of
309 21, *P. daedalea* = 10 of 16), and 18 (56%) were also unique to particular sites. Within
310 *Durusdinium* in the Oman Sea, D5 was the major ITS2 sequence in type profiles in *A. downingi*
311 and *P. daedalea*, while D1 and D17a were dominant in type profiles of *C. microphthalma*. Of the
312 minor *Durusdinium* sequences, 9 (47%) only occurred in a single species (*A. downingi* = 3 of 11,
313 *C. microphthalma* = 3 of 11, *P. daedalea* = 3 of 13).

314

315 Within the dominant Symbiodiniaceae genus hosted by individual coral colonies, ITS2 type
316 profile and sequence associations were generally stable over time (Fig. 3,4). Most colonies
317 sampled more than once over 19 months (74%, $n = 116$), hosted the same sub-generic type profile
318 with the same underlying ITS2 sequences. When temporal variation occurred, this was due to a
319 loss or gain of a minor sequence(s) prompting a shift in ITS2 type profile assignment. For
320 example, differences in the *Cladocopium* type profiles in *A. downingi* between the first two time
321 points (Fig. 3) reflect the loss or gain of C115d and C3b, which were the least abundant sequences
322 within colonies (Table S1). There was no effect of bleaching on type profile associations in the
323 Persian Gulf, except for *C. microphthalma* at Ras Ghanada, where non-bleached colonies all
324 hosted the same type profile, while bleached colonies hosted one of several type profiles (Fig. 4;
325 Table S3). Similarly, there was no effect of bleaching on the community composition of
326 *Cladocopium* sequences (Table S4) or the total diversity of sequences within *P. daedalea* or *C.*
327 *microphthalma* hosts (ANOVA, $F_{1,46} = 0.31$, $P > 0.05$). However, when specific ITS2 sequences
328 were examined, bleaching resistance was strongly linked to the prevalence of the C3gulf variant.
329 On average, the abundance of the C3gulf sequence (relative to the total *Cladocopium* sequences)
330 was 29% higher in non-bleached (0.195 ± 0.016) versus bleached (0.151 ± 0.007) colonies ($t = -$
331 2.49 , Cohen's $D = 0.95$, $P = 0.03$; Table S5). Additionally, the abundance of C3gulf was higher
332 (by up to >500%) for all host species at the two warmest sites (Saadiyat and Ras Ghanada)
333 compared to the cooler site (Delma) within the Persian Gulf (Fig. S6).

334

335 Discussion

336

337 Our results demonstrate that Symbiodiniaceae communities in corals of the Arabian Peninsula
338 exhibit genetic structure that is greatest among regions, followed by host species and individual
339 sites. Previous studies have required the use of several molecular markers to resolve hierarchical
340 patterns of genetic diversity among Symbiodiniaceae genera, species, and populations (e.g. Finney
341 et al., 2010; Santos, Shearer, Hannes, & Coffroth, 2004; Thornhill, Lewis, Wham, & LaJeunesse,
342 2014). Here we show comparable levels of resolution using next-generation sequencing of the
343 multi-copy ITS2 marker and an analysis framework (SymPortal) that incorporates closely related
344 intragenomic variants (Hume et al., 2019). This approach overcomes the issue of evolutionarily

relevant divergence at the ITS2 marker being obscured by a dominance of shared ancestral sequences (Hume et al., 2019; Thornhill et al., 2014).

Coral associations with Symbiodiniaceae genera

We observed strong partitioning of Symbiodiniaceae genera between the southern Persian Gulf and Oman Sea, which confirms the findings of recent studies (D'Angelo et al., 2015; Howells, Abrego, et al., 2016; Ziegler et al., 2017). The dominance of *Cladocopium* (clade C) in the Persian Gulf and *Durusdinium* (clade D) in the Oman Sea in *Acropora downingi*, *Cyphastrea microphthalma*, *Platygyra daedalea* (Fig. 2) has also been documented in several other coral taxa that acquire their symbionts from the environment (Ziegler et al., 2017). In contrast, the same Symbiodiniaceae genus tends to occur in both regions in coral hosts that maternally inherit their symbionts; for example, *Cladocopium* in *Porites*, *Durusdinium* in *Pocillopora*, and *Symbiodinium* (clade A) in *Stylophora* (Ziegler et al., 2017). However, in these instances, partitioning may be apparent at a finer sub-generic level (Hume, D'Angelo, Burt, & Wiedenmann, 2018). For example, *Cladocopium* in *Porites* predominantly belong to the C3 (*C. thermophilum*) group in the Persian Gulf and the C15 group in the Oman Sea (D'Angelo et al., 2015). Similarly, the occasional *Cladocopium* symbionts observed in *C. microphthalma* in the Oman Sea also belonged to the C15 group. Physiological experiments indicate that this consistent regional Symbiodiniaceae divergence across coral hosts is driven by differential tolerance to temperature and salinity, with specialisation of the *C. thermophilum* group to the more extreme conditions of the Persian Gulf (D'Angelo et al., 2015; Howells, Abrego, et al., 2016).

Background (i.e., non-dominant) Symbiodiniaceae genera were more frequently observed in corals from the Persian Gulf, than in the Oman Sea. The occurrence of *Symbiodinium* and/or *Durusdinium* in combination with the dominant *Cladocopium* in the Gulf indicates that the potential for changes in symbiont community composition is not limited by a lack of diversity in this extreme environment (see also Hume et al., 2015; Smith, Vaughan, Ketchum, McParland, & Burt, 2017). Numerous studies have shown a greater prevalence of *Symbiodinium* and *Durusdinium* in health-compromised corals in both the Western Pacific and Caribbean. Increases in the abundance of *Symbiodinium* and *Durusdinium* have been observed in colonies during and after bleaching (heat- and light-induced; Baker, 2001; Jones et al., 2008; Thornhill et al., 2006;

377 Toller, Rowan, & Knowlton, 2001) and in colonies suffering from disease (Rouzé, Lecellier,
378 Saulnier, & Berteaux-Lecellier, 2016; Stat, Morris, & Gates, 2008; Toller et al., 2001). Certain
379 genotypes of these genera presumably displace resident dominant symbionts under adverse
380 conditions due to their comparatively high stress tolerance (LaJeunesse, Smith, Finney, &
381 Oxenford, 2009; Stat et al., 2008). In response to heat stress, shifts to *Durusdinium* dominance can
382 enable colonies to survive and resist subsequent bleaching (Berkelmans & van Oppen, 2006;
383 Silverstein et al., 2015), although the majority of these cases may be limited to a relatively small
384 number of taxa (i.e., *D. trenchii*, (LaJeunesse et al., 2014). However, typical resident
385 Symbiodiniaceae taxa eventually re-establish dominance following the return of normal conditions
386 (e.g. LaJeunesse et al., 2009; Thornhill et al., 2006; Toller et al., 2001). The transient nature of
387 certain associations with *Symbiodinium* and *Durusdinium* genotypes is likely driven by the low
388 rates of photosynthetically fixed carbon transferred to hosts relative to their typical *Cladocopium*
389 and *Breviolum* residents (Cantin et al., 2009; Cunning, Silverstein, et al., 2015; Stat et al., 2008),
390 which negatively impacts coral growth and reproduction (Jones & Berkelmans, 2011; Little et al.,
391 2004; Mieog et al., 2009).

392
393 In our study, the prevalence of *Symbiodinium* and *Durusdinium* was highest in bleached colonies
394 during the 2012 heatwave, particularly at Ras Ghanada (colony abundance up to 54%; Fig 2). In
395 the following summer, a high prevalence of *Symbiodinium* was also observed in *C. microphthalmum*
396 at Ras Ghanada (up to 36%). While these colonies were normally pigmented at the time of
397 sampling, they may have experienced paling early in the summer when temperatures exceeded the
398 local bleaching threshold (34.5°C) for 14 days (Fig. 1b). In both of these instances, the increased
399 prevalence of *Symbiodinium* and *Durusdinium* could be due to opportunistic proliferation of these
400 genera and/or the selective loss of the dominant *Cladocopium* during heat stress. While we cannot
401 distinguish between these possibilities, the absence of *Symbiodinium* and *Durusdinium* in the few
402 colonies that resisted bleaching suggests that proliferation is a more likely explanation. The
403 negative association of *Symbiodinium* and *Durusdinium* abundance with fecundity in *P. daedalea*
404 colonies (Fig. S1) further suggests that genotypes of these genera may also be opportunists in the
405 Persian Gulf. However, further physiological and energetic data are required to support this
406 interpretation. For instance, Gulf genotypes of *Symbiodinium* and *Durusdinium* are likely to be
407 heat tolerant (given their appearance at the warmest sampling times), but it is unknown whether
408 they remain non-preferred symbionts because they also exhibit inferior carbon transfer or whether

409 they suffer disproportionate stress under hypersalinity (~2 PSU higher in winter) and/or winter
410 minimums (<20°C).

411

412 **Coral associations with Symbiodiniaceae ITS2 type profiles and intragenomic variants**

413

414 Within both the Persian Gulf and the Oman Sea, colonies of *A. downingi*, *C. microphthalma*, *P.*
415 *daedalea* hosted unique type profiles and sequences of *Cladocopium* and *Durusdinium* (Figs. 3-5).
416 While coral species shared identical dominant ITS2 sequences (C3 in the Persian Gulf and D5 or
417 D1 in the Oman Sea), the majority of lower abundance intragenomic variants were unique to each
418 coral species. This finding demonstrates that the fine-scale symbiont specificity initially observed
419 among these coral species (Smith, Ketchum, & Burt, 2017) extends across sites and regional
420 divisions in Symbiodiniaceae genera. Similarly, several coral species host unique variants of
421 common ITS2 types in the Caribbean (*Cladocopium* C3, *Breviolum* B1: Finney et al., 2010;
422 Santos et al., 2004; Thornhill et al., 2014) and Western Pacific (*Cladocopium* C3 and C40; Davies,
423 Wham, Kanke, & Matz, 2019) that were previously viewed as “generalist” symbiont taxa (e.g.
424 LaJeunesse et al., 2003). As in these examples, the sympatric divergence of closely related
425 Symbiodiniaceae in the northeastern Arabian Peninsula indicates the specialisation of symbionts
426 to distinct host microenvironments. The fidelity of these partnerships, maintained by recognition
427 and winnowing mechanisms (Fransolet, Roberty, & Plumier, 2012), results in reproductive
428 isolation, and ultimately speciation (Finney et al., 2010; Thornhill et al., 2014). Investigations of
429 fine-scale genetic variation are lacking from Indo-Pacific beyond the Arabian Peninsula (but see
430 Davies et al., 2019), and are required to re-evaluate the generalist nature of ITS2 lineages that are
431 common to many host species. However, it is likely that species-level diversity within the
432 Symbiodiniaceae is currently underestimated.

433

434 For each host species, we observed further spatial structuring of *Cladocopium* sequences in the
435 Persian Gulf. Genetic dissimilarity corresponded with oceanographic distance, where the
436 composition of ITS2 sequences was distinct between the nearby sites of Saadiyat and Ras
437 Ghanada (39 km apart) and most dissimilar from the isolated site of Delma (219-248 km away)
438 (Fig. 5). This fine scale spatial genetic structure is consistent with patterns observed with
439 microsatellite markers for *Cladocopium* populations on the Great Barrier Reef (Howells, van
440 Oppen, & Willis, 2009; Howells, Willis, Bay, & Oppen, 2013) and in the Caribbean (Thornhill et

al., 2014). Thus, it is likely that *Cladocopium* populations in the Persian Gulf are also differentiated due to limited dispersal and recruitment among sites and predominant asexual reproduction within sites (Thornhill, Howells, Wham, Steury, & Santos, 2017). An alternative explanation is that site-specific sequences and type profiles represent functionally distinct genotypes of Symbiodiniaceae that are adapted to local environmental conditions. Adaptation of Symbiodiniaceae populations to local temperatures has been documented (Howells et al., 2012; Pettay & LaJeunesse, 2013), and our sites lie on an east-west gradient in temperature, salinity, irradiance and primary productivity (Howells et al., 2018). However, this interpretation is considered less likely, as environmental and coral community differences between Saadiyat and Ras Ghanada remain very small (e.g. $\leq 0.5^{\circ}\text{C}$ in mean, maximum and minimum temperature; and ≤ 0.3 psu in salinity). A more detailed study is required to fully elucidate *Cladocopium* population genetic structure in the Persian Gulf, ideally incorporating a larger number of sites, and comparing ITS2 intragenomic variation with population genetic markers (i.e., microsatellites or single nucleotide polymorphisms).

The only *Cladocopium* ITS2 sequences common to every coral sample in the Persian Gulf were the pantropical C3 variant and regional C3gulf variant diagnostic of the *C. thermophilum* group (Hume et al., 2015; Hume et al., 2016). Molecular evidence indicates that the prevalence of this stress tolerant group in the southern Gulf has arisen from positive selection acting on rare widespread ancestral variation (Hume et al., 2016). Intriguingly, the variable abundance of C3gulf we observed among samples (2 to 31% of total *Cladocopium* sequences) was highest at the warmest sites and in the small number of colonies that resisted bleaching during the 2012 heatwave (7 unbleached versus 46 bleached colonies; Fig. S5, S6). This suggests that ITS2 intragenomic variation could reflect functional variation within *Cladocopium* populations. In purely clonal populations, each individual cell would be expected to comprise a mixture of intragenomic variants in equal proportions. However, infrequent recombination (Thornhill et al., 2017) and/or somatic mutations (van Oppen, Souter, Howells, Heyward, & Berkelmans, 2011) could result in unequal proportions of intragenomic variants across offspring generations (Wilkinson, Fisher, van Oppen, & Davy, 2015). For example, the co-occurrence of C3 and C3gulf may represent recombination between distinct lineages, with functional differences among purebred, hybrid, and backcross generations (Wilkinson et al., 2015). In support of this interpretation, Wilkinson et al. (2015) documented unequal proportions of ITS2 intragenomic

473 variants among *Cladocopium* cells that were consistent with recombination in colonies of
474 *Pocillopora damicornis* from subtropical Eastern Australia. Furthermore, the physiological
475 performance of *Cladocopium* in these coral colonies corresponded to the intragenomic status of
476 individual cells (i.e., homogenous vs heterogeneous ITS2 sequences; Wilkinson, Brian, Pontasch,
477 Fisher, & Davy, 2018), and spatial differences in the abundance of intragenomically variable cells
478 was associated with a thermal gradient (Wilkinson, Pontasch, Fisher, & Davy, 2016). For
479 *Cladocopium* populations from the Persian Gulf, verifying a role of intragenomic variation in
480 thermal tolerance requires targeted single-celled genotyping and physiological assays that were
481 beyond the scope of this study.

482

483 **Coral symbiosis fidelity and climate warming**

484

485 The Symbiodiniaceae communities in colonies of *A. downingi*, *C. microphthalmum*, and *P.*
486 *daedalea* in the Persian Gulf and Oman Sea remained dominated by the same symbiont genus,
487 type profile, and intragenomic variants over the 1.5 years of this study. This strong fidelity is
488 despite exposure to extreme and seasonally variable temperatures, as well as the elimination and
489 repopulation of symbionts during bleaching. Clearly resident symbionts have an exceptional
490 capacity for thermal acclimation which encompasses both thermal extremes ($>32\text{-}34^{\circ}\text{C}$) and large
491 seasonal changes ($\Delta 11\text{-}16^{\circ}\text{C}$).

492

493 In the hottest reefs in the southern Gulf, it is unclear whether fidelity prevails because corals have
494 already established symbioses with the most tolerant taxa (i.e., the *C. thermophilum* group) or
495 whether alternatives (e.g. regional strains of *Symbiodinium* and *Durisdinium*) are sub-optimal
496 mutualists. The predominant differentiation of *Cladocopium* variants by sympatric host species
497 indicates that selection acts on the coral holobiont to drive mutualistic co-evolution (Laine, 2009).
498 Thus, adaptive responses of symbiont communities to climate warming are conceivably more
499 likely to occur within resident Symbiodiniaceae species (Howells et al., 2012) than by exchange of
500 species and genera. Recent studies show that Symbiodiniaceae populations do exhibit functional
501 variation and thus have the potential to adapt. For example, populations of two *Breviolum* B1
502 species (*B. antillogorgium* and *B. minutum*) from the same host species and reef site encompass
503 standing genetic variation in heat and nutrient tolerance, as well as photosynthesis traits (Bayliss,
504 Scott, Coffroth, & terHorst, 2019). Additionally, a monoclonal culture of *Cladocopium* C1

505 adapted to elevated temperature within 2.5 years (~80 asexual generations) and tended to improve
506 the outcomes for inoculated coral hosts under heat stress (Chakravarti, Beltran, & van Oppen,
507 2017; see also Chakravarti & van Oppen, 2018). While contemporary adaptation in natural
508 Symbiodiniaceae populations remains to be demonstrated, fidelity for specific symbiont partners
509 (i.e., putative species) does not negate the capacity for a symbiont role in coral adaptation.

511

512

513

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515

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524

525 **Authors contributions**

526

527 EJH and AGB conceived the study and CRV designed the molecular approach. EJH, AGB and
528 GOV performed fieldwork. EJH performed molecular work and BCCH and EJH analysed the
529 data. JAB and CRV provided funding and logistical support. EJH wrote the manuscript with initial
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531

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533

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818 **Data availability**

819
820 Raw sequencing data determined in this study are available under NCBI BioProject ID
821 PRJNA532516 (<https://www.ncbi.nlm.nih.gov/bioproject/PRJNA532516>). SymPortal source code
822 releases are published on the Zenodo platform (65).

835 **Figure legends**

836
837 **Figure 1.** The community composition of Symbiodiniaceae was tracked in the corals *Acropora*
838 *downingi*, *Cyphastrea micropthalma*, and *Platygyra daedalea* at five sites in the northeastern
839 Arabian Peninsula (a). Tissue samples were collected from tagged colonies at 5-7 month intervals,
840 at the end of two consecutive summers (2012, 2013) and winters (2013, 2014) (b). Sites
841 experienced seasonal temperature fluctuations between 10-11°C (Oman Sea) and 16°C (Persian

842 Gulf) with summer maxima of 32-35°C and winter minima of 19-22°C. Acute heat stress (coral
843 bleaching) occurred in 2012 at Saadiyat and Ras Ghanada when temperatures exceeded site-
844 specific bleaching thresholds (34.5°C, Shuail et al. 2016; indicated by the dashed horizontal line).
845 Temperature data are daily means from loggers attached to the reef substrate (site gaps = missing
846 data). The base map was sourced from <http://editor.openmaptiles.org>.

847
848 **Figure 2.** The abundance of Symbiodiniaceae genera (clades) within tagged colonies of the corals
849 *Acropora downingi* (a), *Cyphastrea microphthalma* (b), and *Platygyra daedalea* (c) at sites within
850 the Persian Gulf (Delma, Saadiyat, Ras Ghanada) and Oman Sea (Dibba, Al Aqah). Individual
851 colonies, represented by horizontal bars, were sampled in September 2012, April 2013, September
852 2013, and February 2014 (b and c only). Symbols indicate colonies that were moderately bleached
853 (pale, circles) or severely bleached (white, triangles) during the first time point.

854
855
856
857 **Figure 3.** The abundance of *Cladocopium* (clade C) ITS2 type profiles within tagged colonies of
858 the corals *Acropora downingi* (a), *Cyphastrea microphthalma* (b), and *Platygyra daedalea* (c) at
859 sites within the Persian Gulf (Delma, Saadiyat, Ras Ghanada). Individual colonies, represented by
860 horizontal bars, were sampled in September 2012, April 2013, September 2013, and February
861 2014 (b and c only). Symbols indicate colonies that were moderately bleached (pale, circles) and
862 severely bleached (white, triangles) during the first time point. Relationships among type profiles
863 are shown in Fig. S2. In contrast to the C3 dominated type profiles of the Persian Gulf,
864 *Cladocopium* associations in the Oman Sea (in *C. microphthalma*) were comprised of type profiles
865 belonging to C15 (Fig. S2, S3).

866
867 **Figure 4.** The abundance of *Durusdinium* (clade D) ITS2 type profiles within tagged colonies of
868 the corals *Acropora downingi* (a), *Cyphastrea microphthalma* (b), and *Platygyra daedalea* (c) at
869 sites within the Oman Sea (Dibba, Al Aqah). Individual colonies, represented by horizontal bars,
870 were sampled in September 2012, April 2013, September 2013, and February 2014 (b and c only).
871 Relationships among type profiles are shown in Fig. S2. Uncommon low-abundance associations
872 with *Durusdinium* in the Persian Gulf did not belong to divergent type profiles (Fig. S2, S4).

873

874 **Figure 5.** Dissimilarity plot of Symbiodiniaceae ITS2 rDNA sequences belonging to *Cladocopium*
875 (clade C) **(a)** from the Persian Gulf, and **(b)** *Durusdinium* (clade D) from the Oman Sea. Sample
876 profiles (circles) differ by host coral species (*Acropora downingi* = green, *Cyphastrea*
877 *microphthalma* = blue, *Platygyra daedalea* = red) and reef site (colour shade). Principal
878 coordinates analysis was performed on the Bray-Curtis dissimilarities of square-root transformed
879 data of the proportional abundance of unique sequences within each genus.

a **b**

a *Acropora downingi* **b** *Cyphastrea microphthalma* **c** *Platygyra daedalea* *Durusdinium* (clade D) type profile

Sep. 2012

Sep. 2012

Apr. 2013

Sep. 2013

Feb. 2014

Sep. 2012

Apr. 2013

Sep. 2013

Feb. 2014

a Persian Gulf *Cladocopium* (clade C)

b Oman Sea *Durusdinium* (clade D)