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## Species-specific trends in the reproductive output of corals across environmental gradients and bleaching histories

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## ABSTRACT

Coral populations in the Persian Gulf have a reputation for being some of the toughest in the world yet little is known about the energetic constraints of living under temperature and salinity extremes. Energy allocation for sexual reproduction in Gulf corals was evaluated relative to conspecifics living under milder environmental conditions in the Oman Sea. Fecundity was depressed at Gulf sites in two Indo-Pacific merulinid species (*Cyphastrea microphthalma* and *Platygyra daedalea*) but not in a regionally endemic acroporid (*Acropora downingi*). Gulf populations of each species experienced high temperature bleaching at the onset of gametogenesis in the study but fecundity was only negatively impacted in *P. daedalea* and *A. downingi*. Large population sizes of *C. microphthalma* and *P. daedalea* in the Gulf are expected to buffer reductions on colony-level fecundity. However, depleted population sizes of *A. downingi* at some Gulf sites equate to low reef-wide fecundity and likely impede outcrossing success.

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### 1. Introduction

Sexual reproduction is a fundamental life-history process necessary for maintaining population abundance and genetic diversity (van Oppen and Gates, 2006). For many sessile organisms, including reef building scleractinian corals, this mode of reproduction produces dispersive propagules which enable corals to recruit into new habitats and enhance the recovery of populations following disturbances (Hughes and Connell, 1999; Richmond, 1997).

Most coral species are simultaneous hermaphrodites with annual cycles of reproduction culminating in annual broadcast spawning over one or a few consecutive nights (Baird et al., 2009b). Cross-fertilization among colonies is achieved by spawning synchrony and the dispersal potential of lecithotrophic larvae is dependent on oceanographic processes, the onset of settlement competency and the availability of suitable microhabitats for attachment (Figueiredo et al., 2013; Harrison et al., 1984). Environmental cues direct coral larvae to substrata that maintain adequate access to light resources while avoiding sedimentation and algal overgrowth and sessile life commences once metamorphosis is complete (Babcock and Mundy, 1996; Harrington et al., 2004; Hodgson, 1990; Kuffner et al., 2006). Rates of offspring mortality from predation, dispersal to unsuitable habitats and post-settlement processes are extremely large (Connell, 1973;

Fabricius and Metzner, 2004), but are countered by a high investment in fecundity (i.e., gamete production; Ramirez Llodra, 2002).

Fecundity in hermaphroditic corals is typically measured by the number of eggs produced by colony polyps during an annual gametogenic cycle (Wallace, 1985). Egg production requires allocation of finite energy resources which are distributed among survival, growth, lipid storage and reproduction to maximize evolutionary fitness (Ramirez Llodra, 2002). Colony fecundity is positively correlated to colony size, with larger individuals containing more egg producing polyps. Larger individuals also tend to direct more energy to reproduction whereas small individuals invest in growth to maximize survival (Babcock, 1991; Connell, 1973; Kojis and Quinn, 1985). Population fecundity is further determined by the number of reproductively mature colonies, and the proximity of individuals to one another influences outcrossing potential (Lasker et al., 1996; Yund, 2000). Thus, factors that impact the energy resources, size and survival of coral colonies all have downstream influences on fecundity and reproductive success (Hughes et al., 2000).

Multiple disturbances acting simultaneously or in succession can impact energetics and survival in coral populations. These include anomalous temperature events which cause a breakdown of the symbiosis between coral and microalgal partners (i.e. coral bleaching), as well as periodic storm damage, chronic or acute exposure to poor water quality and sedimentation, outbreaks of disease and predation, and altered ecosystem dynamics (Bellwood et al., 2004; De'ath et al., 2012; Hoegh-Guldberg, 1999). Partial and whole colony mortality can have

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long-term and severe effects on fecundity when mature individuals are lost or reduced to immature size-classes (Kojis and Quinn, 1985). Even if rates of new recruitment are high, the onset of first reproduction in corals takes around 3–5 years (Babcock, 1991; Iwao et al., 2010; Wallace, 1985). Additionally, sub-lethal stress can affect the succeeding 1–2 gametogenic cycles by causing reproductive failure or reducing egg numbers and quality (e.g. Baird and Marshall, 2002; Michalek-Wagner and Willis, 2001a, b; Ward and Harrison, 2000). Fecundity exhibits further variation in the absence of disturbance as differences in prevailing environmental conditions among reefs and habitats determine local energy availability and allocation to gametogenesis (Carlon, 2002; Glynn et al., 1991; Kojis and Quinn, 1984; Torrents and Garrabou, 2011).

Coral communities in the southern Arabian/Persian Gulf (hereafter termed “Gulf”) live under marginal conditions for coral growth, with an environment characterized by extremes of temperature and salinity (Kleypas et al., 1999; Riegl and Purkis, 2012; Sheppard et al., 1992). Over the past 20 years, the increased frequency of high temperature events has resulted in recurrent bleaching and/or disease outbreaks occurring at some sites (Coles and Riegl, 2013; Riegl et al., 2011). These events have had a disproportionate effect across taxonomic groups, with substantially greater losses of structurally complex tabular and branching acroporid corals, compared with sub-massive and massive genera such as *Cyphastrea*, *Platygyra* and *Porites* (Burt et al., 2013; Coles and Riegl, 2013). The objective of this study was to assess how prevailing environmental conditions and acute bleaching events affect coral fecundity at both the colony and population level. Fecundity was measured in coral colonies with known bleaching history at multiple sites within the Gulf and compared to conspecifics living in milder and less extreme conditions in the neighbouring Oman Sea (Gulf of Oman). These results extend current baseline data on coral reproduction in these regions (Bauman et al., 2011; Howells et al., 2014) by demonstrating relationships between environmental drivers and species-specific reproductive output.

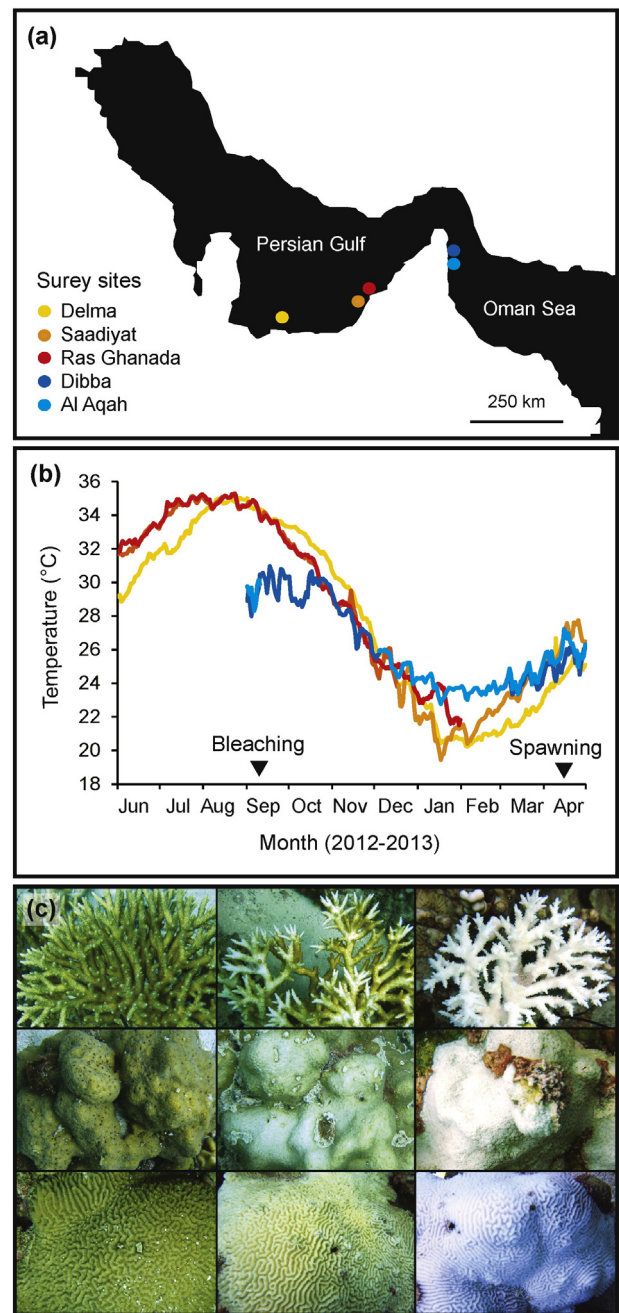
## 2. Materials and methods

### 2.1. Study sites and environmental setting

Coral fecundity was surveyed in three scleractinian coral species (*Acropora downingi*, *Cyphastrea microphthalma*, and *Platygyra daedalea*) common to the Gulf and Oman Sea.

To assess spatial variation in fecundity, 42 to 80 colonies from each species were tagged across 5 survey sites in September 2012 at a depth of 4–7 m (Fig. 1). Southern Gulf sites are characterized by high annual temperature ranges (range: ~15 °C; mean: 27–28 °C; Fig. 1b), high salinity (41–43 ‰), and relatively high turbidity (Riegl and Purkis, 2012; Yao and Johns, 2010). In comparison, Oman Sea sites experience moderate annual temperature ranges (range: ~10 °C; mean: 27 °C), moderate salinity (~37‰) and relatively lower turbidity (Bauman et al., 2013; Yao and Johns, 2010).

To determine whether coral bleaching had an effect on fecundity, the visual pigmentation of coral eggs was recorded at the time of tagging, which coincided with late summer and the start of the gametogenic cycle (Bauman et al., 2011). Bleaching (i.e. paling and whitening) of corals was observed in September 2012 at two sites in the Gulf (Saadiyat and Ras Ghanada). These two sites experienced a greater number of warmer days (20 days of  $\geq 35$  °C) than the remaining Gulf site (Delma, 1 day at 35 °C; Fig. 1b). In the Oman Sea, summer temperatures rarely exceed 33 °C and no bleaching was observed in 2012. The bleaching condition of all colonies was visually assessed and classified as: healthy (dark pigmentation), moderately bleached (pale pigmentation) or severely bleached (white pigmentation; Fig. 1c). To determine whether colony size affected fecundity, the maximum length and width of each colony was measured. Given that colony size was not the primary interest in this study, a complete range of size classes was not targeted during sampling.



**Fig. 1.** Site location (a), temperature profiles (b) and bleaching condition (c) of coral colonies surveyed for reproductive output in the Persian Gulf and Oman Sea. Temperature profiles at each site were recorded using *in situ* temperature loggers attached to the reef substrate (gaps in profiles are periods where loggers went missing). Bleaching condition images were taken from the Persian Gulf sites the September 2012 bleaching event and are representative of *Acropora downingi*, *Cyphastrea microphthalma* and *Platygyra daedalea* colonies (top to bottom) classed as healthy, moderately bleached and severely bleached (left to right).

### 2.2. Colony fecundity

Fecundity was quantified in 77% of tagged colonies that were resampled two weeks before the peak coral spawning period in April 2013 (Bauman et al., 2011; Howells et al., 2014; Table 1). Tissue samples (5–10 cm<sup>2</sup>) were collected from the centre of each colony in order to avoid sterile colony edges. Gamete maturity was then evaluated using egg pigmentation scores where samples containing pink (*A. downingi* and *P. daedalea*) or pale orange (*C. microphthalma*) coloured eggs (80%

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