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REVIEW

Sexual production of corals for reef restoration in the Anthropocene

Carly J. Randall[1,*], Andrew P. Negri[1], Kate M. Quigley[1], Taryn Foster[2], Gerard F. Ricardo[1], Nicole S. Webster[1,3], Line K. Bay[1], Peter L. Harrison[4], Russ C. Babcock[5], Andrew J. Heyward[2]

[1]Australian Institute of Marine Science, PMB 3, Townsville, QLD 4810, Australia
[2]Australian Institute of Marine Science, Indian Ocean Marine Research Centre, University of Western Australia, Crawley, WA 6009, Australia
[3]Australian Centre for Ecogenomics, University of Queensland, Brisbane, QLD 4072, Australia
[4]Marine Ecology Research Centre, Southern Cross University, Lismore, NSW 2480, Australia
[5]Oceans and Atmosphere, Commonwealth Scientific and Industrial Research Organisation, St Lucia, QLD 4072, Australia

ABSTRACT: Coral-reef ecosystems are experiencing frequent and severe disturbance events that are reducing global coral abundance and potentially overwhelming the natural capacity for reefs to recover. While mitigation strategies for climate warming and other anthropogenic disturbances are implemented, coral restoration programmes are being established worldwide as an additional conservation measure to minimise coral loss and enhance coral recovery. Current restoration efforts predominantly rely on asexually produced coral fragments — a process with inherent practical constraints on the genetic diversity conserved and the spatial scale achieved. Because the resilience of coral communities has hitherto relied on regular renewal with natural recruits, the scaling-up of restoration programmes would benefit from greater use of sexually produced corals, which is an approach that is gaining momentum. Here we review the present state of knowledge of scleractinian coral sexual reproduction in the context of reef restoration, with a focus on broadcast-spawning corals. We identify key knowledge gaps and bottlenecks that currently constrain the sexual production of corals and consider the feasibility of using sexually produced corals for scaling-up restoration to the reef- and reef-system scales.

KEY WORDS: Coral reproduction · Sexual reproduction · Coral restoration · Gametogenesis · Embryogenesis · Spawning · Settlement · Climate change

1. INTRODUCTION

Up to half of the world's tropical corals have been lost in the last 50 yr (Pandolfi et al. 2003, Wilkinson 2008, Burke et al. 2011, De'ath et al. 2012, Hughes et al. 2017, 2018), and over one-third of scleractinian coral species are now at increased risk of extinction (Carpenter et al. 2008). Three pan-tropical mass-bleaching events occurred in the last 4 decades — including unprecedented back-to-back bleaching and mortality events on the Great Barrier Reef (GBR) in 2016 and 2017 — collectively signalling an acceleration in global reef decline (Sweet & Brown 2016, Hughes et al. 2018). The increasing frequency, intensity, and spatial scale of these thermal-stress events no longer allows sufficient time between disturbances

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*Corresponding author: c.randall@aims.gov.au

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for coral communities to recover to their pre-disturbance cover and composition (Osborne et al. 2017, Hughes et al. 2018, Lough et al. 2018, Ortiz et al. 2018). Furthermore, coral-bleaching events are no longer constrained to years with extreme El Niño–Southern Oscillation (ENSO) conditions (Hughes et al. 2018), and are affecting reefs regardless of conservation status and management regime (Selig et al. 2012), leading to calls for additional action, including direct restoration interventions (see Anthony et al. 2017, van Oppen et al. 2017). At present, active coral restoration is spatially limited (e.g. Hein et al. 2017), and coral restoration programmes targeting entire reefs and reef systems will require new approaches to re-establish ecosystem functions at ecologically relevant scales.

Most coral restoration programmes to date have leveraged the clonal structure of coral colonies and utilised 'coral gardening' techniques, whereby corals are fragmented or microfragmented (asexually) and outplanted onto degraded reefs or artificial reef structures (Bowden-Kerby 2003, Rinkevich 2005, 2008, Forsman et al. 2006, 2015, Shaish et al. 2010, Johnson et al. 2011, Young et al. 2012, Lirman & Schopmeyer 2016). An alternative, and increasingly advocated approach, is to generate and deploy sexually produced corals (e.g. Heyward et al. 2002, Edwards & Gomez 2007, Harrison 2011, Nakamura et al. 2011, Guest et al. 2014, Omori & Iwao 2014, Chamberland et al. 2015, 2017, Harrison et al. 2016, dela Cruz & Harrison 2017, Pollock et al. 2017, Omori 2019, see also www.secore.org).

Future restoration approaches involving the mass production of corals are likely to benefit from combining traditional asexual propagation methods with advances in the sexual production of corals. Firstly, collecting sexual propagules while leaving adult colonies on the reef is a more ecologically sustainable approach. Secondly, the use of sexual propagules from spawning events is arguably the most cost-effective and feasible way to produce the large numbers of corals required for restoration (Edwards 2010, Doropoulos et al. 2019). Finally, and perhaps most importantly, approaches using sexual reproduction promote genetic diversity, which is central to species conservation (Baums 2008, van Oppen et al. 2015, 2017). The sexual generation of corals also enables selective breeding of individuals with potentially advantageous traits, such as temperature tolerance (van Oppen et al. 2017), which may already exist in bleaching survivors and populations from naturally extreme or marginal environments (e.g. Barshis et al. 2013, Howells et al. 2016a). Given the rapid and accelerating rates of environmental change associated with increasing greenhouse-gas emissions, it is essential to maintain and potentially enhance the acclimatisation and adaptation potential supported by high genetic diversity within existing coral populations. Consequently, restoration programmes that produce corals sexually have started to gain momentum over the last decade.

In this review, we summarise the current state of knowledge of sexual reproduction in scleractinian corals within the context of reef restoration, with a focus on broadcast spawning, which is both the dominant mode of sexual reproduction and currently is more amenable to large-scale larval culture than the collection of planulae from brooding species. Additional information from studies of brooding corals is included where relevant. We highlight key knowledge gaps and bottlenecks in the coral life cycle where human intervention may optimise or accelerate processes for application in reef restoration. We also summarise key knowledge needs to guide research in the broader coral restoration community, and consider the feasibility of recovering the structure and function of degraded coral reefs through interventions with sexually produced corals.

2. THE CORAL LIFE CYCLE

Scleractinian corals have a biphasic life cycle composed of a dominant sessile, benthic polyp phase and a motile planula larval phase (our Fig. 1; Harrison & Wallace 1990, Richmond & Hunter 1990, Harrison 2011). Polyps form the basic unit of a coral colony, and the polyp phase is dominated by somatic growth and asexual budding that creates new and genetically identical polyps. Once a coral colony reaches an adequate size and age, a cycle of sexual reproduction commences (Fig. 1).

The modes of sexual reproduction have been identified for approximately half of the estimated 900 extant species of hermatypic scleractinians (Veron 2000), and 4 general patterns have emerged: (1) hermaphroditic broadcast spawning; (2) hermaphroditic brooding; (3) gonochoric broadcast spawning; and (4) gonochoric brooding (Fadlallah 1983, Harrison 1985, 2011, Richmond & Hunter 1990, Baird et al. 2009, Madin et al. 2016). While most corals with known reproductive patterns follow one of these strategies, some species do not conform to the typical dichotomies (i.e. brooding vs. spawning and hermaphroditic vs. gonochoric; Harrison 2011, Guest et al. 2012), and it is likely that the diversity of recorded reproductive patterns will continue to increase as more taxa are studied.

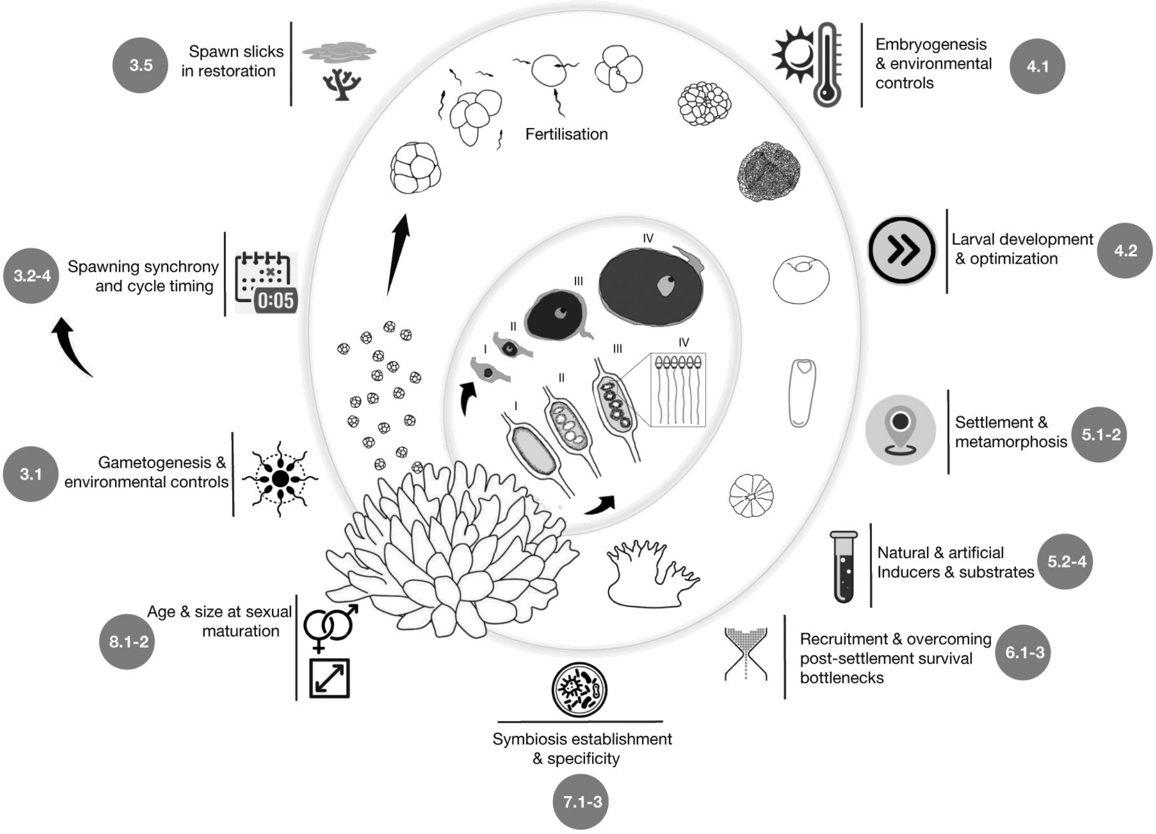

Fig. 1. Stages of broadcast-spawning coral life cycle (after Jones et al. 2015), with stages of gametogenesis in the centre (after Vargas-Ángel et al. 2006). Text sections of the present paper are indicated by the numbers in the filled grey circles, and key restoration research priorities for each developmental stage are indicated with icons as defined in Table 2. Gametes develop within or attached to mesenteries that contain oocytes and/or spermatocytes and progress through 4 stages, over several months or more (I–IV; e.g. Szmant-Froelich et al. 1980, Szmant-Froelich 1985, Harrison & Wallace 1990, Glynn et al. 1991, Vermeij et al. 2004, Madsen et al. 2014). Oocytes (top row of inner cycle) begin as enlarging interstitial cells adjacent to, or within, the mesenterial mesoglea (Stage I; Madsen et al. 2014), and slowly accumulate cytoplasm around the nucleus (Stage II). Over time, oocytes increase in size, and yolk forms around the nucleus (vitellogenesis, Stage III), with final maturation (Stage IV) occurring as the cortical layer and vitelline membrane are complete, as the yolk granulates and the egg becomes visibly pigmented in many species, and finally as the nucleus moves toward one side of the egg (Stage IV). Sperm development (bottom row of inner cycle) begins with the clustering of spermatogonia adjacent to, or within, the mesoglea (Stage I), which is followed by meiosis and the development of distinct spermatocytes with large nuclei in Stage II. The number of spermatocytes and spermatids within the spermary increases during Stage III as meiosis continues, and they become peripherally arranged with prominent central lacunae. In Stage IV, spermatids have little cytoplasm, develop a flagellum, and arrange themselves in bouquet arrays within the spermaries

Gonochoric species have separate sexes, while hermaphroditic corals develop both eggs and sperm within polyps or colonies. Most hermaphroditic corals are simultaneous hermaphrodites, while some are sequential (Harrison 2011), and a few exhibit bidirectional sex change (i.e. Loya et al. 2009, Eyal-Shaham et al. 2019). Broadcast-spawning corals release gametes into the water column for external fertilisation and larval development. Brooders typically undergo internal fertilisation and release well-developed planula larvae, although some species produce asexually brooded larvae (Harrison 2011). Over 80% of species whose reproductive modes are known spawn gametes for external fertilisation (Baird et al. 2009, Harrison 2011).

3. GAMETOGENESIS, SPAWNING, AND REPRODUCTIVE SYNCHRONY

Coral reproductive cycles are aligned with environmental conditions that improve survival and fitness. Environmental conditions can regulate reproductive cycles in 2 ways: as ultimate factors, which exert evolutionary selective pressures to maximise reproductive success (Babcock et al. 1986, Harrison

& Wallace 1990, Oliver et al. 1998), and as proximate factors, which cue and synchronise cycles. Ultimate factors include seasonal temperature cycles that may optimise physiological performance (Babcock et al. 1986, Keith et al. 2016), wind speeds (van Woesik 2010, Heyward & Negri 2012) and tidal phases (Babcock et al. 1986, 1994) that may maximise fertilisation success and dispersal, and diurnal cycles that may allow for predator avoidance (Harrison et al. 1984). In the context of coral restoration, we are unlikely to be able to manipulate ultimate factors, and doing so is risky and may decrease fitness. Therefore, we focus here on proximate factors that act mechanistically, which are more amenable to experimental manipulation, and that are most relevant to restoration.

Proximate factors that synchronise gametogenic and spawning cycles (Fig. 1) are thought to be regulated by a hierarchy of exogenous environmental cues (e.g. annual, seasonal, lunar, and daily, as detailed in the following sections) that interact with endogenous biorhythms at successively finer timescales to optimise reproductive success (Harrison & Wallace 1990, Hoadley et al. 2016). There is a rapidly growing understanding of the endogenous and molecular mechanisms that underpin reproductive cycles and synchronisation (e.g. Sorek et al. 2014, Kaniewska et al. 2015, Hoadley et al. 2016), which shows great promise for our ability to manipulate gametogenesis and spawning for restoration. However, it is critical that such manipulations retain the reproductive characteristics of wild populations to allow for interbreeding with existing populations after deployment.

3.1. Annual and seasonal controls of gametogenesis

For most broadcast spawners, gametogenesis follows an annual cycle; oogenesis takes place slowly, over multiple months (4–12 mo), while spermatogenesis occurs more quickly (1–8 mo), with sperm maturation coinciding with the final stages of oogenesis, usually a few days or weeks prior to an annual-spawning event (our Fig. 1; Wallace 1985, Szmant 1986, Harrison & Wallace 1990, Vermeij et al. 2004, Vargas-Ángel et al. 2006, Chin et al. 2014). However, multiple gametogenic cycles per year have been described in some coral populations (e.g. Stobart et al. 1992, Penland et al. 2004, Mangubhai & Harrison 2008a), and many brooding species have several overlapping gametogenic cycles each year (Kojis 1986, Szmant 1986, Harrison & Wallace 1990, Foster & Gilmour 2018), with some releasing larvae on a daily basis (Nietzer et al. 2018).

Temperature has long been considered an important factor governing reproductive seasonality and often is correlated with gametogenic cycles in broadcast spawners and some brooders (Shlesinger & Loya 1985, Babcock et al. 1986, Kojis 1986, Hayashibara et al. 1993, Vargas-Ángel et al. 2006, Nozawa 2012, Keith et al. 2016). Oogenesis usually commences asynchronously during cooler periods in autumn or winter months (Wallace 1985, Szmant 1986, Harrison & Wallace 1990, Vargas-Ángel et al. 2006); then, as seawater temperatures rise rapidly in mid-spring, oocyte diameter increases and oocytes gradually develop from Stage I through Stage IV, culminating in synchronised maturation (Stage IV) during periods of warm seawater temperatures (our Fig. 1, inner cycle; Wallace 1985, Willis et al. 1985, Szmant 1986, Vargas-Ángel et al. 2006, Madsen et al. 2014, Keith et al. 2016). While temperature clearly affects the rates of physiological processes in corals, it likely plays a secondary role in determining the timing of spawning, either by affecting growth and final maturation directly (Nozawa 2012) or through interactions between endogenous clock mechanisms (e.g. Kaniewska et al. 2015) and temperature.

Solar insolation is another important cue that synchronises gametogenesis, particularly for equatorial corals that experience a small annual range in seawater temperatures (Penland et al. 2004, van Woesik et al. 2006, Brady et al. 2009). Light is thought to entrain oscillations of a molecular clock (~24 h periodicity) through 2 interacting transcription/translation feedbacks that form an endogenous rhythm, the ‘speed’ of which is in synchrony with seasonal changes in day length (Hoadley et al. 2016). Light acts as a proximate cue for reproduction, but is also a fundamental energy source driving reproductive effort. Reduction in solar insolation with increasing latitude or water depth may constrain reproductive effort, resulting in protracted gamete development (i.e. ‘slower speeds’) and lower overall fecundity (Kojis & Quinn 1984, Harii et al. 2001, Feldman et al. 2018, Shlesinger et al. 2018).

While spawning usually occurs once per year in a synchronous-spawning event, it can also be protracted, occurring as sequential events over several months and seasons (Shlesinger & Loya 1985, Heyward 1987, Hayashibara et al. 1993, Penland et al. 2004, Mangubhai & Harrison 2008b, Fogarty et al. 2012, Bouwmeester et al. 2015). Biannual spawning within coral populations has been observed in Western Australia (Gilmour et al. 2009, 2016), and split-spawning — a form of asynchrony that occurs somewhat predictably every 2–3 yr — happens either when the same colony spawns over 2 or 3 consecutive months, or when different colonies from the same population spawn on successive lunar cycles (Willis et al. 1985, Mangubhai & Harrison 2008b, Baird et al. 2009, 2012, Foster et al. 2015, 2018, Gilmour et al. 2016).

3.2. Lunar controls of spawning

Remarkably, gamete release within species can be synchronised to within minutes, and often is restricted to a single night of the year. Within seasons, spawning is correlated with the lunar cycle and is likely cued directly by moonlight detected through photoreceptors (possibly cryptochromes or opsins, see Hoadley et al. 2016) that sense moonlight intensity (Levy et al. 2007, Kaniewska et al. 2015, but see Linden et al. 2018). Some brooding species may use similar processes to coordinate planulae release, whereas other brooders do not exhibit lunar periodicity in planulation (Jokiel et al. 1985, Vermeij et al. 2003, Zakai et al. 2006, Linden et al. 2018, Nietzer et al. 2018). No data are available on photosensitivity of cnidarian cryptochromes; however, they may form part of the circadian clock rather than serve as photosensors (Hoadley et al. 2016). Manipulating the day of spawning or planulation based on offset artificial moonlight cycles could be used to distribute coral production in aquaculture facilities throughout the month, reducing bottlenecks in culture processes that could occur when relying on single monthly spawnings. Manipulating lunar and seasonal temperature and light cycles to split spawning across months also could potentially increase coral production in controlled aquaculture systems.

3.3. Diel controls of spawning

While several species have been observed to spawn during daylight (e.g. Mangubhai et al. 2007, Eyal-Shaham et al. 2019), the final and shortest temporal cue for the majority of spawning species is the time after sunset on the night of spawning; conspecifics consistently spawn a certain number of minutes to hours after sunset (Willis et al. 1985, Babcock et al. 1986, Vize 2006), and similar diel cycles of planulae release are evident among some brooding species (Jokiel et al. 1985, Fan et al. 2006). This timing can persist even following artificial induction of gamete release (Hayashibara et al. 2004) and when diel cycles are offset to manipulate the timing of spawning (Babcock 1984). This behaviour is directly controlled by local photoperiod and does not appear to be entrained by a biological clock (Brady et al. 2009).

3.4. Predicting and controlling gametogenesis and spawning for restoration

Identifying the underlying drivers of synchronous spawning among more taxa will enable the efficient and reliable production of a greater diversity of coral species for restoration. For example, more reliable information about spawning cycles for daytime or dawn spawners (e.g. Bronstein & Loya 2011, Eyal-Shaham et al. 2019) would allow production effort to be spread across species throughout the day and night, and identification of multiple spawning events within a population (e.g. Stobart et al. 1992) could provide additional opportunities throughout the year for spawn collection. Furthermore, reliably obtaining spawned gametes from other important coral taxa (beyond reliance on acroporid and merulinid species) is important to retain functional diversity of restored ecosystems.

Manipulation of endogenous rhythms and optimised aquaculture conditions may underpin future hatchery-style production of corals. Practitioners could (1) maintain multiple populations on off-set annual cycles to produce gametes several times per year, (2) accelerate gametogenesis so that 1 population can be spawned several times per year, and (3) control the hour of spawning to spread effort throughout the day. Research has already begun to test the feasibility of some of these options. Firstly, by artificially mimicking seasonal and daily insolation cycles, lunar-irradiance cycles, and seasonal temperature fluctuations, Craggs et al. (2017) replicated natural gametogenic cycles in GBR corals that were transported and maintained for >1 yr in an aquarium in the UK. This is a first step in maintaining synchronously spawning populations in artificially controlled environments. Secondly, maintaining optimal light intensity to support photosynthesis and providing additional food sources for corals *ex situ* may partly overcome nutrient limitations for gametogenesis, allowing for multiple gametogenic cycles per year (e.g. Szmant-Froelich et al. 1980).

There may be potential trade-offs, however, between increased gamete production and other vital processes such as somatic-tissue growth, calcification, and immune responses (Harrison & Wallace 1990). Furthermore, the quality and viability of gametes resulting from nutrient enrichment may be inferior to those produced under natural conditions, and thus further investigation is needed prior to implementation in any restoration programme (e.g. Ward & Harrison 2000). Lastly, the long-term effects of out-of-season-spawned corals on future spawning synchrony and fitness are not known and must be investigated.

3.5. Capturing spawn slicks for restoration

Synchronously spawning corals, with colony fecundities reaching 10^6 m^{-2} (e.g. Álvarez-Noriega et al. 2016, Howells et al. 2016b), may release billions of eggs and sperm per hectare of reef. Under calm conditions, these positively buoyant eggs can form highly concentrated and species-rich surface slicks (our Fig. 2a; Butler 1980, Oliver & Willis 1987), and if the gametes are healthy, could provide a natural source of sexually produced propagules for restoration (Kawaguti 1940, Heyward et al. 1999, Omori & Fujiwara 2004, Harrison et al. 2016).

Spawn slicks are generally pink or white in colour and can be observed as discrete patches or narrow strips on the sea surface extending several kilometres from a reef (Butler 1980, Oliver & Willis 1987). The size and location, the species composition, the viability, and the longevity of a slick are all closely tied both to oceanographic and environmental conditions and to coral composition and abundance. When and where slicks will form, and how long they persist, is controlled by surface oceanographic features, such as eddies or fronts between water bodies (Wolanski & Hamner 1988, Jones et al. 2006), and is dependent on wind speed. Wind speeds between 2 and 4 m s^{-1} are associated with the highest probability of slick formation (Romano & Marquet 1991, van Woesik 2010), while slicks are unlikely to form at wind speeds above 6–7 m s^{-1} (Romano 1996). Although coral spawning often occurs during calm periods (van Woesik 2010), weather monitoring over a decade at selected reefs on the GBR showed that wind speed exceeded 5 m s^{-1} for ~50% of major spawning events (Heyward & Negri 2012). Similarly, in the Philippines, slight differences in local turbulence from year to year have influenced the extent of slick formation and their speed of dispersal (Jamodiong et al. 2018). Therefore, local meteorological and oceanographic conditions during coral spawning have important roles in predicting slick formation at a given reef.

The species composition and viability of the slick are closely tied to the abundance of adult corals on the reef from the most fecund spawning families, such as Acroporidae and Merulinidae. The biological and physical attributes of propagules, including oocyte diameter, buoyancy, and developmental rate, also vary by species and consequently affect the propensity of each species to end up in slicks. A slick sample from the GBR, for example, contained early-stage larvae, in a size range mostly between 200 and 800 µm, with modal peaks around 400 and 550 µm and a mean diameter of 484 µm (Fig. 2b,c), indicating a diversity of species. Extrapolation from these sizes to a calculation of packed cell volume suggests that a dense surface slick just 1 mm thick could contain several million eggs, embryos, or larvae per square metre, although viability within slicks can be highly variable (Oliver & Willis 1987). Poor viability in some slicks may be caused by rainfall creating low-salinity stress (Harrison et al. 1984, Richmond 1993) or anoxic conditions in the surface layer from microbial decomposition of spawn, caused by either low fertilisation success or sequential days of spawning (Simpson et

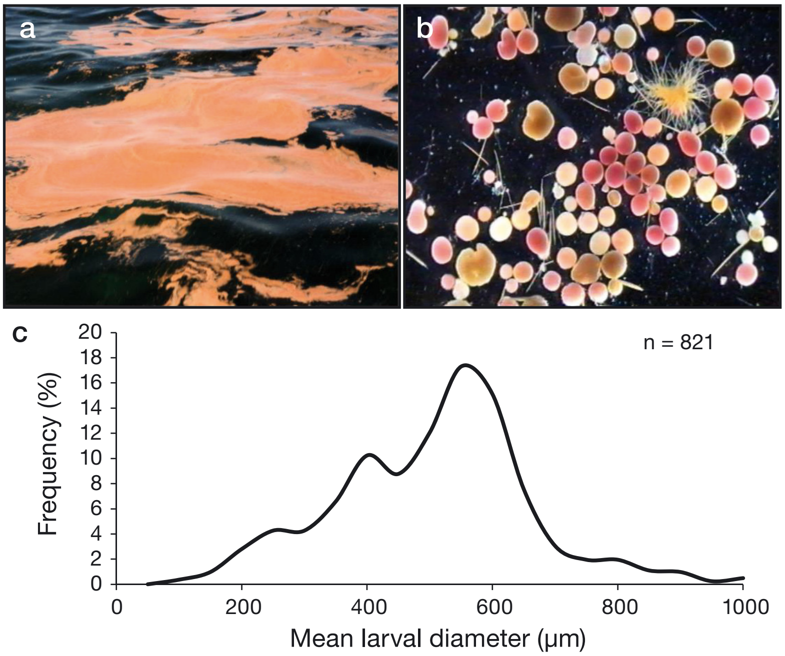

Fig. 2. (a) Multi-species coral surface slick at Lizard Island, at 07:00 h, the morning after spawning. (b) Photomicrograph of a sample from the surface slick in (a), showing various coral embryos and larvae and other flotsam. (c) Coral larval size–frequency distribution measured from the slick shown in (a,b). 'n' in (c) indicates the number of larvae measured to estimate the size–frequency distribution. Photos: A. Heyward

al. 1993, Guillemette et al. 2018). Because the formation, size, and viability of slicks are influenced by the abundance of adult colonies, the accessibility of coral slicks for restoration may diminish in parallel with a decline in coral abundance.

Spawn slicks could be utilised in restoration by: (1) holding a slick above a target reef to mimic natural retention and increase recruitment (e.g. Golbuu et al. 2012, Harrison et al. 2016); (2) collecting and transporting larvae from a slick to a recruitment-limited reef location for release (Heyward et al. 1999, 2002, dela Cruz & Harrison 2017, Doropoulos et al. 2019); or (3) collecting and settling larvae from a slick onto artificial substrates for grow-out and deployment (e.g. Chamberland et al. 2017). Efforts to collect and deliver captive larvae back to the reef and manipulate larval settlement have so far utilised floating ponds and hoses (Heyward et al. 2002, Omori et al. 2004), mesh enclosures (dela Cruz & Harrison 2017), tents (Edwards et al. 2015), plastic bags (Suzuki et al. 2012), foam ring-seeder devices (Cooper et al. 2014), and Perspex boxes (Quigley et al. 2018b). However, coral restoration programmes targeting entire reefs and reef systems would need to implement such methods at much larger scales than have previously been attempted (Doropoulos et al. 2019).

In early trials, harvested wild slicks produced competent larvae in Western Australia (Heyward et al. 2002) and Okinawa (Omori et al. 2004). Those studies, and subsequent restoration efforts using captive-spawned larvae in Palau (Edwards et al. 2015) and the Philippines (dela Cruz & Harrison 2017), demonstrated enhanced settlement rates through increased larval supply. Nonetheless, increased settlement rates on artificial surfaces did not elevate the numbers of surviving 1 yr old corals above that observed in adjacent areas with natural recruitment in Palau (Edwards et al. 2015). In contrast, larval enhancement on 4 replicate 24 m^2 degraded reef plots with low natural recruitment in the Philippines increased recruitment rates of *Acropora tenuis* compared with reference plots, and re-established a breeding population within 3 yr (dela Cruz & Harrison 2017). These examples demonstrate that a positive outcome from larval restoration is possible in some situations, but the cost-effectiveness and scalability of this approach remain challenging.

There is a limited period for the capture of a surface slick with concentrated and viable embryos and larvae. Coral embryos are structurally fragile during the first hours of development (Heyward & Negri 2012) but become more robust after gastrulation. Consequently, careful isolation and containment of a slick may be feasible in the hour or 2 immediately after spawning, prior to cleavage (which may be protracted for multi-species slicks), but otherwise is best delayed until the cohort is at least 24 h old (Omori & Fujiwara 2004). Subsequently, a period of days (but generally not weeks) is available for culture and transport. Extended transit times risk larval settlement during transport, particularly for cultures of brooded larvae, which are usually released at an advanced larval stage and are competent to settle quickly after release. Therefore, slick harvesting should consider larval viability and concentration at or near the surface, bearing in mind early embryo fragility and changes to larval distribution in the water column during development (Section 4.1). These trade-offs provide several technical challenges for the future large-scale use of slicks for coral restoration.

4. EMBRYOGENESIS AND LARVAL DEVELOPMENT

Embryogenesis and larval development are among the most sensitive processes in the coral life cycle (Figs. 1 & 3). Understanding where and when these processes take place, the risks and sensitivities associated with these stages, and their environmental drivers will allow culture conditions to be optimised for the *ex situ* production of corals.

4.1. Environmental controls on embryogenesis and larval development

Early embryogenesis (our Fig. 3f–h; first cleavage through blastula) usually occurs overnight at the sea surface (Babcock & Heyward 1986, Hayashibara et al. 1997, Ball et al. 2002, Okubo & Motokawa 2007, Okubo et al. 2013, 2017). The lipid-rich embryos of most species (Arai et al. 1993) are positively buoyant and passively transported, while cilia develop on the outer surface, leading to 'rotary' swimming. The timing of the onset of rotary swimming varies across species but can occur as early as 12 h (e.g. *Pavona decussata*) or as late as 3 d (e.g. *Pseudosiderastrea* spp.) after fertilisation (Okubo et al. 2013). Directional swimming of the larvae is achieved hours to days after rotary swimming, when they begin exhibiting phototactic responses and become capable of adjusting their positions in the water column (our Fig. 3j,k; Lewis 1974, Harrison & Wallace 1990). The timing of larval competency for settlement also varies across species (reviewed in Jones et al. 2015) and can occur as early as 24 h after spawning (e.g. *Fungia fungites*) or can require a week or more of larval development (e.g. *Acropora austera*).

Environmental factors that affect fertilisation success and can cause embryonic abnormalities include elevated inorganic nutrient concentrations (reviewed in Fabricius et al. 2005, Humphrey et al. 2008, Lam et al. 2015, Richmond et al. 2018), $p\mathrm{CO_2}$ (Albright 2011, Albright & Mason 2013), sediments (reviewed in Jones et al. 2015), and pollutants (reviewed in Hudspith et al. 2017). Rates of embryogenesis are also temperature-dependent; warm temperatures have been shown to accelerate development in several species, including acroporids and mussids (Bassim et al. 2002, Bassim & Sammarco 2003, Negri et al. 2007, Randall & Szmant 2009a, Heyward & Negri 2010, Chua et al. 2013, Graham et al. 2017). Warmer ocean temperatures can also reduce fertilisation success (Negri et al. 2007, Albright & Mason 2013) and increase the likelihood of embryonic abnormalities, leading to increased mortality (Bassim et al. 2002, Bassim & Sammarco 2003, Negri et al. 2007, Randall & Szmant 2009a,b). In a study of *Acropora palmata*, a 4°C increase in temperature decreased larval survival by ~60%, with most losses occurring during the process of gastrulation (Randall & Szmant 2009a).

Coral embryos lack the protective external membrane of some other metazoans; hence, early embryonic stages are fragile and readily fragment into smaller groups of cells (Heyward & Negri 2012). During windy and turbulent conditions, for example, early morulae (2–16-cell stages; Fig. 3m) can fragment and then continue cleaving, eventually developing into proportionally smaller larval clones, sometimes one-eighth the normal size (Heyward & Negri 2012). The deliberate fragmentation of early embryos to generate smaller larvae in culture may increase larval numbers and compress the larval competency period, as smaller larvae generally reach competency sooner (Figueiredo et al. 2013). However, larger fragments (blastomeres) are more likely to survive, and the resulting small recruits may be disadvantaged, as the time required to grow to size-escape thresholds may be longer (Raymundo & Maypa 2004, Doropoulos et al. 2012b). Furthermore, only fragments with animal hemispheres can develop into primary polyps (Okubo et al. 2017).

4.2. Optimising embryogenesis and larval development for restoration

In culture, direct handling of embryos should be minimised, and mass cultures should initially have no aeration and slow water movement for the first 18–24 h, unless deliberately generating small embryos (Edwards 2010, Omori & Iwao 2014, Pollock et al. 2017). Aeration and water flow can be increased once embryos reach the gastrula stage (our Fig. 3i) ~12–24 h post-fertilisation (Okubo et al. 2013).

Exposure to elevated-temperature conditions during early-life histories is a potential tool for accelerating development (Nozawa & Harrison 2000, 2007, Randall Szmant 2009a, Heyward & Negri 2010) and enhancing the thermal tolerance of restored corals (Putnam & Gates 2015, van Oppen et al. 2015, 2017). Nonetheless, possible benefits of accelerated rates of development and stress-hardening may be countered by lower fertilisation rates, higher rates of developmental abnormalities, disease, mortality, and downstream consequences on general culture health. Thermal tolerance selection through stress-hardening of coral larvae, and its role in long-term acclimatisation, have not yet been quantified, and thus constitute critical research priorities.

5. SETTLEMENT AND METAMORPHOSIS

The successful recruitment of corals includes both settlement (Section 5) and post-settlement survival (Section 6), and reef restoration would benefit from the optimisation of both processes.

5.1. Larval sensory systems and the processes of settlement and metamorphosis

The transition from a motile planula larva to a sessile polyp (i.e. ‘settlement’) is a multi-stage process that includes selection of a settlement substrate, followed by attachment to that substrate, metamorphosis from larva to polyp, and finally acquisition of photosymbionts (Section 7) for those species that acquire them from the environment (Harrison & Wallace 1990). Although planktonic larvae are transported by ocean currents, they can vertically modulate their position in the water column (Tay et al. 2011), which increases their likelihood of intercepting reef substrate (Raimondi & Morse 2000, Szmant & Meadows 2006). Once at or near the seabed, larvae (whether from spawning or brooding species) sense the substratum and actively search for a suitable attachment site (reviewed in Gleason & Hofmann 2011, Jones et al. 2015) using a range of sensory capabilities (our Fig. 4; Young 1995). These sensory capabilities comprise the detection and discrimination of light fre-

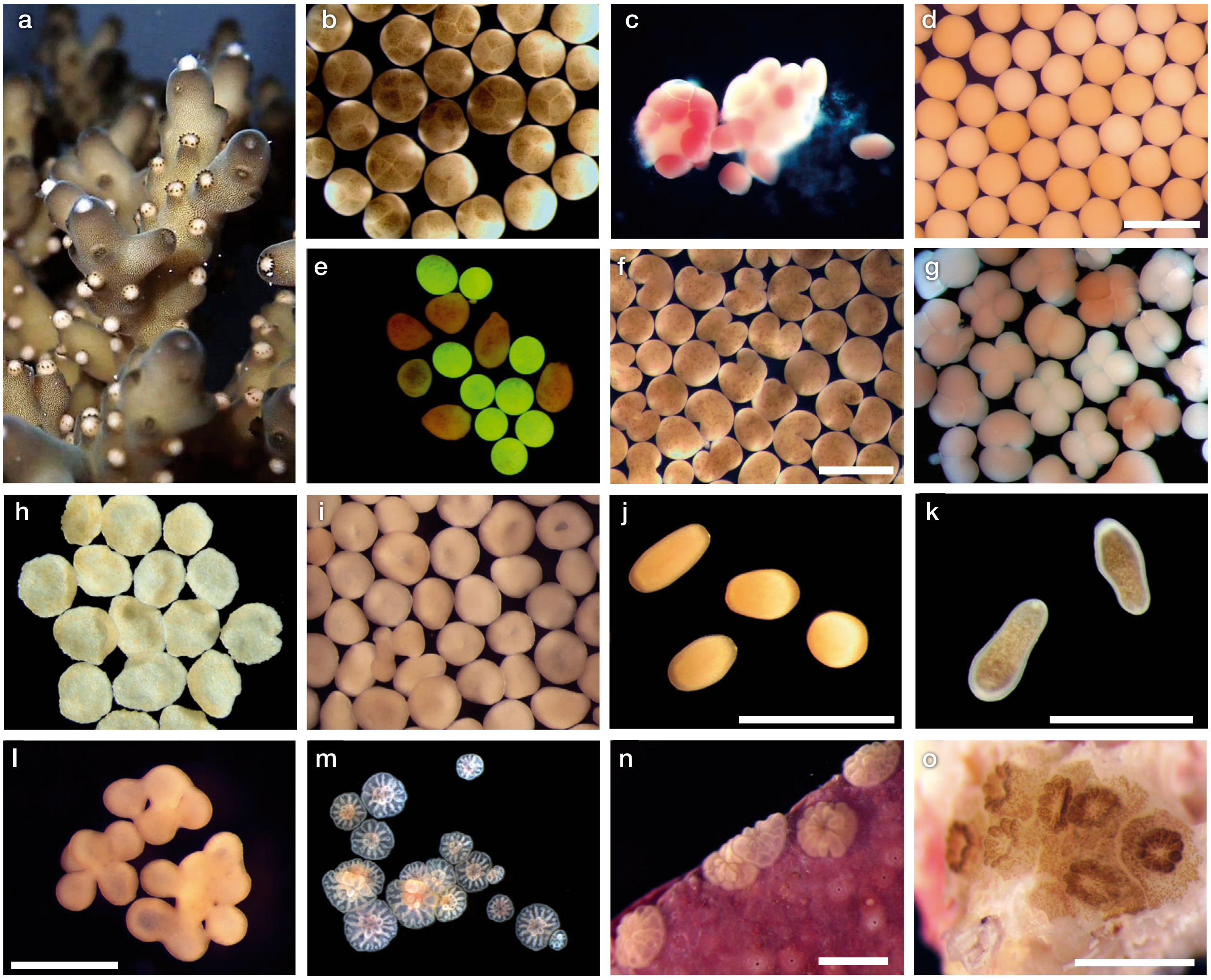

Fig. 3. Coral developmental stages. (a) Egg–sperm bundles setting inside mouths of polyps in *Acropora loripes.* (b) Intact, packed egg–sperm bundles of *Montipora digitata* immediately after release. (c) *Acropora longicyathus* egg–sperm bundles dissociating, releasing individual eggs and sperm from the bundle centres. (d) Unfertilised eggs of *A. spathulata* after 30 min of rounding out. (e) Unfertilised eggs of *M. digitata* under fluorescence microscopy showing variable green-fluorescent protein signals. (f) Early cleavage of fertilised *M. digitata* eggs. Note the presence of endosymbiotic dinoflagellates in these vertical transmitters. (g) *A. tenuis* 3 h after fertilisation in early cleavage. (h) Delicate 'prawn-chip' stage of *Montipora capitata* 15 h after fertilisation. Note the presence of endosymbiotic dinoflagellates. (i) *A. loripes* 16 h after fertilisation, rounding out into the gastrula stage. (j) *Platygyra daedalea* larvae beginning to elongate. (k) Fully developed and competent larvae of *M. digitata* with dense endosymbionts. Note the fully differentiated epidermis that lacks symbionts. (l) *Mycedium elephantotus* chimeras formed from the fusion of 4–8 individual embryos. (m) *A. millepora* recruits of various size classes resulting from fragmentation of blastomeres of 2-, 4-, or 8-cell embryos during early cleavage. (n) *A. spathulata* spat (single polyps) 2 d post-settlement. Note the absence of endosymbionts. (o) *Montipora digitata* coral spat settled in an aggregation, 2 d post-settlement. Note the presence of endosymbionts. Scale bars = 1 mm. Photos in (a), (g), and (m): Andrew Negri; (c): Andrew Heyward; (b), (d–f), (h–l), and (n,o): Carly Randall

quencies (Lewis 1974, Babcock & Mundy 1996, Mundy & Babcock 1998, Strader et al. 2015), gravity, hydrostatic pressure (Stake & Sammarco 2003), possibly sound (Vermeij et al. 2010), and biochemical signals (Morse et al. 1996, Negri et al. 2001, Gleason et al. 2009, Tebben et al. 2015) (our Fig. 4). While the larvae of many coral species require a chemical cue of biological origin (inducer or morphogen) to induce settlement, this may not be a stringent requirement for all corals, as larvae of some species appear to settle spontaneously (Loya 1976, Harrison & Wallace 1990, Baird & Morse 2004). A broad range of cues (Section 5.2) can initiate settlement. Receptors on the ovoid larva detect the cues, and this triggers a cas-

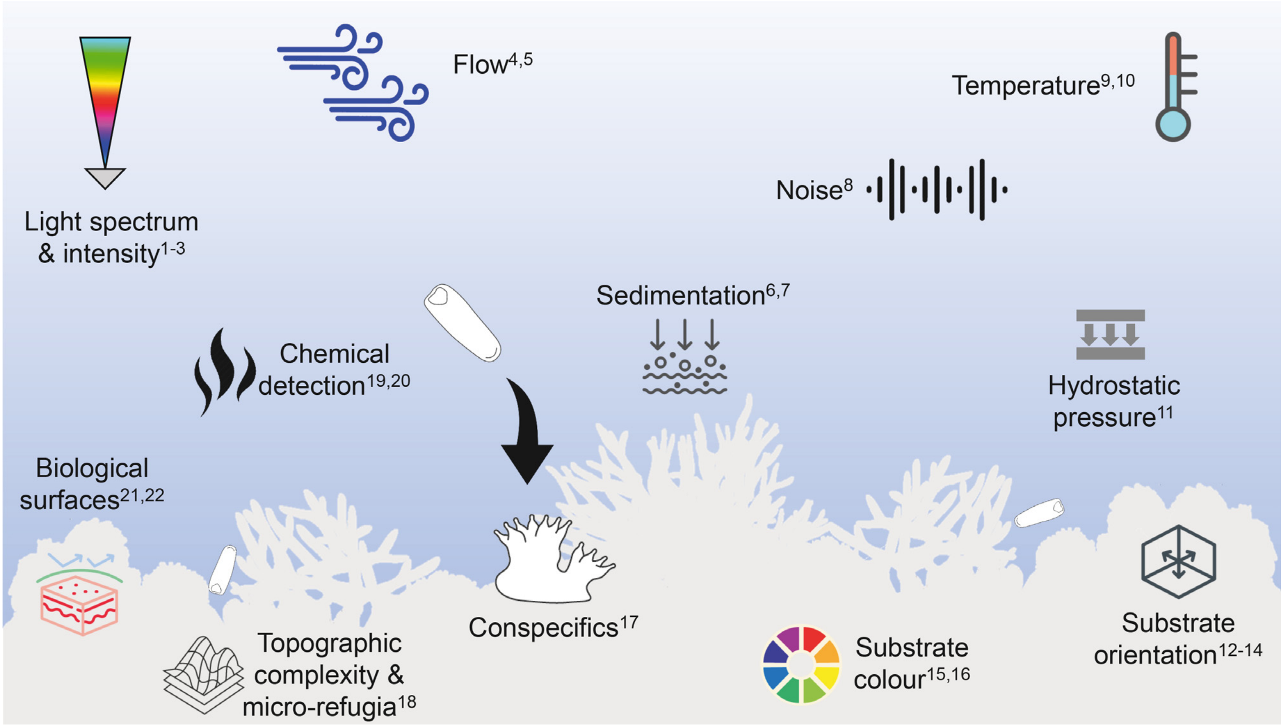

Fig. 4. Schematic diagram of the general physical, chemical, and biological factors (cues) that guide larvae to settlement locations and influence and trigger larval settlement on the reef, with example references for each factor. [1]Babcock & Mundy (1996), [2]Mundy & Babcock (1998), [3]Strader et al. (2015), [4]Roberts (1997), [5]Hata et al. (2017), [6]Babcock & Davies (1991), [7]Jones et al. (2015), [8]Vermeij et al. (2010), [9]Edmunds et al. (2001), [10]Randall & Szmant (2009a), [11]Stake & Sammarco (2003), [12]Goreau et al. (1981), [13]Doyle (1975), [14]Fadlallah (1983), [15]Mason et al. (2011), [16]Foster & Gilmour (2016), [17]Da-Anoy et al. (2017), [18]Whalan et al. (2015), [19]Tebben et al. (2015), [20]Gleason et al. (2009), [21]Morse et al. (1996), [22]Negri et al. (2001)

cade of internal biochemical and molecular signals (Grasso et al. 2011) that result in attachment of the aboral end, and initiation of metamorphosis into a sessile polyp (our Fig. 3m–o; Harrison & Wallace 1990).

The time to settlement competency in larvae of broadcast spawners is species-specific and may follow a normal distribution within a cohort. Typically, first settlement is observed around 3 d after spawning at water temperatures of 26–28°C (Connolly & Baird 2010, Figueiredo et al. 2013, Jones et al. 2015), with a majority competent within 4–6 d. By contrast, brooded larvae often may settle within a few hours after release from parent polyps, although some planulae remain competent for months (Stephenson 1931, Harrigan 1972, Shlesinger & Loya 1985, Richmond 1987, Harrison & Wallace 1990).

Metamorphosis of most species occurs within 24 h of substrate attachment (but see Nozawa & Harrison 2000), when the larva has morphed into a disc-shaped structure with 6 incipient mesenteries radiating outward from a central mouth (Figs. 1 & 3m–o). Tentacles usually become apparent within 48 h (our Fig. 3o; Harrison & Wallace 1990, Heyward & Negri 1999). While metamorphosis usually closely follows attachment, the cues for attachment and metamorphosis can be distinct and temporally uncoupled, with attachment occurring days to weeks before metamorphosis (e.g. *Platygyra daedalea*, Nozawa & Harrison 2000; some *Acropora* species, Harrison 2006).

The hierarchy of cues, from subtle physical signals to strong and specific chemical inducers, also differs among species, enabling larvae to identify species-specific settlement sites that may optimise post-settlement survival and fitness (Morse et al. 1988, Raimondi & Morse 2000, Baird et al. 2003, Baird & Morse 2004, Golbuu & Richmond 2007, Gleason & Hofmann 2011). Settlement on light-exposed upper surfaces, for example, may favour energy acquisition via photosynthesis by symbionts; however, in this orientation, the ~1 mm juvenile polyps may be more prone to predation, overgrowth by algae, and smothering by sediments (Vermeij 2006, Gleason & Hofmann 2011, Jones et al. 2015). Attachment of larvae to dark undersurfaces may reduce these hazards, but could cause reduced growth from light limitation or competition from encrusting taxa. A successful strategy for the acroporids is to settle near underside edges somewhat protected from predation, grazing, and physical dislodgement, yet receiving enough light to promote colony growth (Mizrahi et al. 2014, dela Cruz & Harrison 2017). Larvae of many species also favour settling in microrefugia such as in corners, crevices, or hollows of similar size to their diameter (Petersen et al. 2005, Nozawa 2008, Okamoto et al. 2008, Doropoulos et al. 2012b, 2016, Whalan et al. 2015). Older juveniles, however, tend to be found on exposed surfaces, reflecting the strong influence of post-settlement mortality on determining adult coral distributions (Babcock & Mundy 1996, Mizrahi et al. 2014, Doropoulos et al. 2016, dela Cruz & Harrison 2017).

5.2. Settlement cues and inhibitors

Larval settlement can be triggered by a broad range of abiotic cues, including surface topography (Whalan et al. 2015) and colour (Mason et al. 2011, Foster & Gilmour 2016); however, biochemical inducers produced by crustose coralline algae (CCA) (our Fig. 3n; Morse et al. 1996, Harrington et al. 2004, Tebben et al. 2015) and microbial biofilms (Harrigan 1972, Webster et al. 2004, Tran & Hadfeld 2011, Sharp et al. 2015) are considered more influential in triggering settlement in many species (Gleason & Hofmann 2011, Jones et al. 2015). Choice experiments have demonstrated clear coral–algal specificity for some species (Morse et al. 1996, Harrington et al. 2004, Ritson-Williams et al. 2010, 2016, Davies et al. 2014); e.g. *Acropora* spp. larvae settle at higher rates on cryptic *Titanoderma prototypum* (Harrington et al. 2004). Less-preferred CCA species may overgrow the juvenile coral or shed surface layers, resulting in the dislodgement of the coral (Harrington et al. 2004).

The specific components of CCA and biofilms that induce settlement remain elusive. Reported chemical inducers associated with CCA include a sulphated glycosaminoglycan (Morse & Morse 1991), a macrodiolide (Kitamura et al. 2009), glycoglycerolipids and polysaccharides (Tebben et al. 2015), and mixtures of a bromotyrosine derivative and carotenoids (Kitamura et al. 2007). Tetrabromopyrrole (TBP) isolated from the biofilm bacterium *Pseudoalteromonas* sp. induces rapid metamorphosis in some species, but is not always preceded by attachment and is relatively unstable (Tebben et al. 2011, Sneed et al. 2014). Similarly, the neuroactive signalling peptide GLW-amide induces metamorphosis in acroporid corals and can be readily synthesised, but permanent attachment of larvae is not always achieved (Iwao et al. 2002, Erwin & Szmant 2010, Tebben et al. 2015).

A range of toxicants, including metals, pesticides, petroleum products, and other industrial products, have been shown to impact larval settlement (Negri & Heyward 2000, Reichelt-Brushett & Harrison 2000, Negri et al. 2005, Lam et al. 2015, Hudspith et al. 2017), and the physical blocking of cues can impede settlement as well. A very thin layer of sediment, for example, can prevent settlement on substrates with strong cues, and when removed, a legacy impact on the inductive capacity of the substrate may remain (Ricardo et al. 2017). Elevated temperature and $p\mathrm{CO}_2$ exposure can also directly reduce settlement rates and increase post-settlement mortality (Randall & Szmant 2009a,b, Albright et al. 2010, Heyward & Negri 2010, Albright & Langdon 2011, Doropoulos et al. 2012a, but see Putnam et al. 2008), but can also negatively impact the biota that induce coral settlement, causing the broad-scale impairment of natural recruitment (Kuffner et al. 2008, Doropoulos et al. 2012a, Webster et al. 2013, Fabricius et al. 2015, 2017).

5.3. Optimising coral settlement for restoration

Understanding the cues, and particularly the biochemical inducers, that control larval settlement can facilitate the attachment of mass-cultured larvae onto natural or artificial substrata for restoration.

Successful settlement on any surface typically follows 'biological conditioning' for several weeks, for the development of microbial biofilms and recruitment of CCA (Harrigan 1972, Harrison & Wallace 1990, Webster et al. 2004), or artificial induction (Guest et al. 2014, Omori & Iwao 2014, Chamberland et al. 2017). Small (~5 mm) chips of live or dead CCA have reliably been used to attract and trigger larval settlement onto surfaces in experimental studies (Morse et al. 1996, Heyward & Negri 1999) and this method could be applied to settle cultured larvae onto most natural and artificial surfaces for deployment in restoration. However, scaling-up this process requires the harvesting or culturing of CCA, and the species used may not actively induce settlement of all target species (Baird & Morse 2004, Davies et al. 2014).

Applying natural biochemical inducers from CCA and biofilms onto surfaces for reef rehabilitation has been considered for over 2 decades (D. E. Morse et al. 1994, A. Morse et al. 1996). This approach is dependent on extracting the active chemicals produced by the CCA or biofilm and immobilising the chemicals on a surface (D. E. Morse et al. 1994, A. Morse et al. 1996). The application of these chemicals to artificial surfaces for reef restoration would require mass isolation or synthesis of complex biochemicals, which can be unstable and costly, and none have so far proven to have universal activity across species. The application of natural and artificial inducers to settle larvae en masse requires more fundamental research, and currently, field or laboratory conditioning of surfaces to develop multi-species CCA and bacterial biofilms represents a less controlled but more feasible approach to settle a diversity of larvae for restoration.

Site selection by competent larvae is an important consideration for larval reseeding. Changes in settlement behaviour commence in the water column before a physical encounter between a larva and the substrate occurs, where waterborne chemicals associated with benthic organisms or pollutants may attract or repel them. Because allelopathic effects can extend well beyond the substrate boundary layer (Birrell et al. 2005, 2008, Morrow et al. 2016), they may drive larval selection or rejection of a settlement site. The degree to which larvae are capable of actively selecting among settlement sites through vertical positioning, however, is a matter of debate (Baird et al. 2014, Dixson et al. 2014, Hata et al. 2017), and may be limited to a small spatial scale, and to the crawling phase after the larvae have contacted the substrate.

Given the highly sensitive nature of larvae to physical, biological, and chemical agents, it is critical to evaluate and mitigate potential settlement inhibitors, particularly at a site where recruitment of larvae is a core restoration strategy (Beyer et al. 2018). The risks posed by settlement inhibitors at candidate restoration sites can be quantified by comparing *in situ* water quality measurements with thresholds derived from laboratory assays. In addition, there is mounting evidence that stressors and inhibitors can interact cumulatively to reduce coral settlement (Humanes et al. 2017) and thus should be considered in the selection and management of sites for restoration.

5.4. Artificial substrates for use in reef restoration

The artificial substrate most suitable for reef restoration depends on the goal and scale of the project (Spieler et al. 2001, Chamberland et al. 2015, 2017, Barton et al. 2015), and practitioners should consider the effectiveness, cost, environmental impact and the feasibility of use in large-scale applications. Almost any solid material can be used to settle coral larvae; however, materials differ in their composition and succession of colonising communities, resulting in differences in their abilities to attract and induce metamorphosis, and to reduce competition with other benthic organisms. For example, ceramic tiles are widely used for assessing settlement *in situ*, in part because they provide colonising CCA with a competitive advantage over other encrusting and fouling organisms (Harriott & Fisk 1987). As settlement cues are often species-specific, the settlement surface and subsequent successional biofouling community likely bias the settling-coral community.

The shape and topography of artificial substrates can be designed and manufactured to produce an optimal settlement habitat. Larvae are drawn to small crevices and areas free of sediments and grazers (our Section 5.1; Babcock & Davies 1991, Doropoulos et al. 2016, Ricardo et al. 2017). Several organisations are developing ‘seeding units’ designed to maximise recruitment success by incorporating natural microrefugia (e.g. Chamberland et al. 2017). Past restoration projects have improved recruit survival by using grates, meshes, or poles that provide a range of angles for settlement, while also allowing sediments to pass through (Omori et al. 2006, Suzuki et al. 2011, Higa & Omori 2014, Ng et al. 2016). Three-dimensional printing technology is increasingly applied to help replicate the complex shapes of naturally occurring reefs (Mohammed 2016). Not all materials are easily shaped, however, and malleability and ease of manufacture of complex surfaces to improve restoration success need to be carefully considered.

Ease of deployment and suitability for the receiving environment are also important considerations. Substrates that need to be manually and individually attached to the seafloor (e.g. small recruitment substrates) are likely to be the most expensive and least practical to up-scale. By contrast, substrates that can be deployed from the surface with less effort, such as tetrapods designed to maximise the chance of wedging into the reef structure and increase retention (Chamberland et al. 2017), could be more economical at scale, noting that ideal substrates may vary by environment. Finally, it is imperative to consider the potential long-term environmental and ecological impacts of the selected material before introduction into the environment, where it may act as, or generate, pollution or marine debris. Some plastics have been associated with coral diseases (Lamb et al. 2018), and microplastics generated from the breakdown of plastics in the marine environment impact many organisms, including corals (Hall et al. 2015, Reichert et al. 2018).

6. RECRUITMENT AND POST-SETTLEMENT SURVIVAL

Early post-settlement survival is a primary bottleneck and challenge for coral restoration. Coral spat are particularly susceptible to predation, competition, and stochastic disturbances, and need to grow quickly to escape this vulnerable phase. Most newly settled corals are also aposymbiotic and must establish symbioses with a suite of partners to survive. Reducing predation and competition for young restored corals, both directly and indirectly, and providing recruits with targeted symbiotic partners, represent opportunities to overcome this bottleneck.

6.1. Density-dependent processes in recruitment and post-settlement survival

Settlement success can increase with larval density (Heyward et al. 2002, Suzuki et al. 2012, Doropoulos et al. 2018), but dense cultures may be suboptimal for larval health (Guest et al. 2010, Pollock et al. 2017) or carry downstream risks. Higher larval densities can increase gregarious settlement (our Fig. 3m, o) up to a density-dependent parabolic threshold (Suzuki et al. 2012, Doropoulos et al. 2017, 2018), which can accelerate growth and improve survival to a point (Suzuki et al. 2012). The availability of substrate with appropriate settlement cues can also interact with density-dependent biological processes; clustered patterns in the benthic community can encourage the clustering of spat around a settlement cue. On degraded reefs, a reduction in quality substrate may further encourage clustered settlement around rare cues and promote density-dependent recruitment bottlenecks (Vermeij & Sandin 2008, Albright et al. 2010, dela Cruz & Harrison 2017, Fabricius et al. 2017).

Mortality in the first year after settlement can be extremely high (>30–99%) (Loya 1976, Babcock 1985, Babcock & Mundy 1996, Wilson & Harrison 2005, Davies et al. 2013, Suzuki et al. 2018). Stochastic processes like accidental grazing and storms contribute significantly to juvenile mortality (Mumby 1999, Davies et al. 2013, Trapon et al. 2013), and the drivers of mortality shift with life stage and size. For example, small juveniles 1–2 mo old are more susceptible to accidental grazing (Trapon et al. 2013) compared with larger 10–14 mo old juveniles (Davies et al. 2013). Generally, mortality pressures continue to act on coral juveniles until they reach a size-escape threshold, or size refuge, when mortality significantly declines (Babcock & Mundy 1996, Doropoulos et al. 2012b, dela Cruz & Harrison 2017). This size refuge may differ across species but can be around 5 mm in diameter or 3–9 mo old (Babcock & Mundy 1996, Doropoulos et al. 2012b). Furthermore, juvenile mortality after settlement can vary in a density-dependent manner. Dense settlement, for example, may lead to higher predation through predator attraction (Gallagher & Doropoulos 2017), or alternatively could lead to decreased predation by reaching size-escape thresholds more quickly (Raymundo & Maypa 2004, Doropoulos et al. 2012b).

6.2. Maximising post-settlement survival in reef restoration

A variety of methods have been proposed to either reduce predation on, or competition with, spat to overcome post-settlement survival bottlenecks for coral restoration. Firstly, substrates have been engineered with multiple surface orientations and microtopography, such as corners, crevices, holes, and divots, to offer a refuge from accidental grazing and to limit sedimentation impacts (Nozawa 2008, Chamberland et al. 2017). Materials with embedded antifouling compounds that target and prevent direct competition from other benthic organisms are being explored (Tebben et al. 2014), as are materials that have unpalatable embedded compounds that aim to reduce grazing pressure and deter corallivores.

Secondly, co-culturing techniques have been trialled, whereby coral recruits or fragments are reared alongside grazers, in a multi-trophic aquaculture system, and then deployed together. For example, co-culturing of coral spat with herbivorous gastropods such as *Trochus* spp. and *Clypeomorus* spp. snails (Omori 2005, Villanueva et al. 2013, Omori & Iwao 2014, Toh et al. 2016) and echinoderms (Toh et al. 2016, Craggs et al. 2019) has been found to increase spat survival. Thus, herbivorous gastropods, echinoderms, and fishes, which already are routinely used to control algae in large-scale coral nurseries, offer opportunities for enhanced production efficiency. Furthermore, Spadaro (2014) reported preliminary success in deploying large herbivorous brachyuran crabs with high site fidelity at coral restoration locations in the Caribbean, indicating that *in situ* co-culturing also may be beneficial at restoration sites.

6.3. Size matters: improving restoration outcomes with chimeras

Coral larvae tend to settle gregariously (our Fig. 3m,n) and occasionally form natural chimeras (Amar et al. 2008, dela Cruz & Harrison 2017), which can rapidly increase the size of the juvenile by an order of magnitude, and accelerate growth to the size-escape threshold (Raymundo & Maypa 2004, Doropoulos et al. 2012b, 2018, Suzuki et al. 2012). Chimeras develop from the fusion of genetically distinct coral embryos (our Fig. 3l; Jiang et al. 2015), juveniles (our Fig. 3m,n; e.g. Raymundo & Maypa 2004, Amar et al. 2008) or adults (Puill-Stephan et al. 2009), and may confer several ecological advantages such as faster growth, earlier sexual maturation, and increased competitive ability (Rinkevich & Weissman 1987, 1992, Puill-Stephan et al. 2009, Rinkevich et al. 2016). The fusion of *Pocillopora damicornis* larvae resulted in higher growth and survival of juveniles (Raymundo & Maypa 2004), and chimeras produced from brooded *Stylophora pistillata* larvae exhibited increased survival compared with individual juveniles (Amar et al. 2008). Yet, the ability of corals to discriminate self from non-self (allorecognition) and to tolerate chimeric colonies varies among species. Allorecognition in corals is driven by mechanisms of genetic histocompatibility (Heyward & Collins 1985, Heyward & Stoddart 1985, Stoddart et al. 1985), which develop as juveniles mature (Hidaka 1985, Hidaka et al. 1997). Chimerical full-sibling juveniles tend to exhibit the highest rates of stable post-settlement survival compared with half and non-sibling juveniles (Nozawa & Loya 2005, Puill-Stephan et al. 2012b), and chimera formation at the larval or early recruit stage, before the maturation of immune recognition mechanisms, can increase fusion success (Hidaka 1985, Hidaka et al. 1997, Wilson & Grosberg 2004, Puill-Stephan et al. 2012a,b, Schweinsberg et al. 2015). Thus, forming chimeras from related individuals early in ontogeny, during the embryo and larval stages, is likely to have the best outcome. Whether coral chimera formation can be controlled to yield a net increase in surviving recruits remains an area of current research (Cooper et al. 2014, Barton et al. 2015, Forsman et al. 2015).

7. CORAL SYMBIOSES

Central to a healthy coral are relationships with associated microorganisms, which have profound implications for coral health, stress tolerance, and acclimation response (Mieog et al. 2009). Mutually beneficial symbioses with photosynthetic dinoflagellates (Symbiodiniaceae, sensu LaJeunesse et al. 2018) and enduring partnerships with an array of bacterial, archaeal, fungal, protistan, and viral associates together form the coral holobiont (Bourne et al. 2016). Understanding when and how coral symbioses are established, and the capacity for these relationships to be manipulated and maintained is an active area of research in coral restoration.

7.1. Establishment, maintenance, and specificity of symbiotic partnerships

The most well studied coral symbionts are dinoflagellates of the family Symbiodiniaceae with densities $>10^6$ cells cm^{-2} providing up to 90% of the coral's nutritional requirements through translocation of photosynthates and other essential nutrients (Muscatine & Porter 1977). The amount of carbon and nitrogen translocated to the coral host, however, can vary substantially among species and Symbiodiniaceae clades (Yellowlees et al. 2008, Davy et al. 2012, Tremblay et al. 2014) and under different environmental conditions (Little et al. 2004, Reynolds et al. 2008, Cantin et al. 2009, Hume et al. 2015). Bacterial and archaeal symbionts also occur at densities as high as 10^6 cells cm^{-2} (Garren & Azam 2012), with the diversity of these prokaryotic communities often exceeding thousands of distinct taxa (Sunagawa et al. 2010, Blackall et al. 2015). While these microbes cycle essential nutrients (carbon, nitrogen, sulphur, and phosphate) and provide trace metals, vitamins, and other cofactors (Bourne et al. 2016), examples of specific prokaryotic symbionts being unequivocally assigned functional roles are rare.

Early molecular studies indicated that some coral species form exclusive partnerships with a single Symbiodiniaceae type, whereas other species are known to associate with multiple types that vary in their relative abundance over time and space (Little et al. 2004, Abrego et al. 2009a,b, Fabina et al. 2012, Byler et al. 2013, Boulotte et al. 2016, Poland & Coffroth 2017). These symbionts can be shared via parental gametes (i.e. vertical transmission), assimilated solely from the surrounding environment (i.e. horizontal transmission), or acquired through a mixture of both strategies (Byler et al. 2013, Quigley et al. 2018a). Vertical transmission of a locally adapted Symbiodiniaceae community may benefit species with localised dispersal (Underwood et al. 2007, Sherman 2008, Noreen et al. 2009, Warner et al. 2016), but could also be disadvantageous if environmental conditions change or if larvae are dispersed to novel environments. Alternatively, a horizontally acquired community may offer more flexibility under variable environmental conditions (Abrego et al. 2012, Boulotte et al. 2016, Quigley et al. 2017a, 2018a). Genetic analyses of relatedness and preferential selection experiments, however, have demonstrated that for both transmission modes, Symbiodiniaceae communities are, at least in part, regulated by their host and are not random (Yamashita et al. 2014, Quigley et al. 2017a, 2018a).

For most coral species, the exact point at which a Symbiodiniaceae symbiosis is initiated, and the environmental origins of horizontally transmitted symbionts, remain unclear. Symbiodiniaceae, which can also be free-living, have been recovered from seawater and substrates of coral reefs, but their diversity and availability for host uptake is not well known (Adams et al. 2009, Cumbo et al. 2013, Quigley et al. 2017b). Larvae and juveniles of some *Acropora* species can establish symbiosis with Symbiodiniaceae shortly after exposure to local sediments (Adams et al. 2009, Cumbo et al. 2013). Yet, the diversity of Symbiodiniaceae residing within sediments is much greater than the diversity in corals, indicating that juvenile corals selectively uptake Symbiodiniaceae and/or certain types and sizes have higher infectivity (Yamashita et al. 2013, 2014, 2018, Biquand et al. 2017, Quigley et al. 2017b).

How the Symbiodiniaceae community changes during juvenile development is also poorly understood. For example, the brooding coral *Porites astreoides* showed substantial variation in the Symbiodiniaceae community throughout ontogeny and under different environmental conditions (Reich et al. 2017). Yet, parental effects (e.g. the influence of the maternal environment during gamete development) also explain a significant amount of the variation in symbiont composition in the spawning species *Acropora tenuis* (Quigley et al. 2016). Thus, it remains largely unknown how flexible or deterministic the host–symbiont community is for the vast majority of coral species.

The mode of transmission of prokaryotic symbionts, including bacterial, archaeal, fungal, protistan, and viral associates, constitutes a critical research priority. There is some indication that brooding species transmit at least some of these symbionts vertically, whereas species that rely on external fertilisation acquire many of these symbionts horizontally (Apprill et al. 2009, Sharp et al. 2012). However, spawning corals can vertically transmit some components of the microbiome via mucus contact during spawning (Leite et al. 2017), and coral-associated bacteria can exhibit chemotaxis towards chemicals released from the coral, which likely influences the establishment and maintenance of species-specific host–microbe interactions (Tout et al. 2015).

7.2. Environmental control over symbiotic partnerships

Symbiotic partnerships between corals and microorganisms are sensitive to environmental perturbations, and symbiotic dysbiosis (i.e. imbalance) can represent a significant challenge to coral survival. The ability of some species to establish flexible partnerships with tolerant symbionts (Symbiodiniaceae or bacteria), however, could confer a plasticity that underpins transgenerational acclimatisation (Webster & Reusch 2017). For instance, juvenile *Acropora* species can increase the relative abundance of tolerant Symbiodiniaceae under higher seawater temperatures (Abrego et al. 2012, Yorifuji et al. 2017), while some adult corals can acquire increased thermal tolerance by changing their dominant Symbiodiniaceae type (Berkelmans & van Oppen 2006). At higher seawater temperatures, the larvae of some species can establish symbiosis with novel and thermally tolerant symbionts, while reducing their association with heat-sensitive Symbiodiniaceae (Cumbo et al. 2018). Furthermore, corals containing thermally tolerant algal symbionts are much more abundant on reefs that have been severely affected by recent climate change (Baker 2003, Baker et al. 2004), and Symbiodiniaceae associations can vary by host depth and light conditions (Iglesias-Prieto et al. 2004, Bongaerts et al. 2013, Nitschke et al. 2018).

The environmental sensitivity of coral-associated bacterial communities is also well established, with a shift towards opportunistic microorganisms and potential pathogens under ocean warming and ocean acidification (reviewed in Bourne et al. 2016). This sensitivity has been primarily documented with adult corals, with little understanding of microbial responses in early life-history stages. Furthermore, while the loss of symbionts has been correlated with declining host health, there are few examples of favourable symbiotic bacterial shifts that enhance growth or confer a competitive advantage under environmental change.

7.3. Controlling symbiont communities in restored corals

Although there is some support for symbiont switching in adult corals (Boulotte et al. 2016, Quigley et al. 2019), early juveniles may be the opportune age to initiate infection with both environmentally tolerant Symbiodiniaceae communities, and beneficial-bacterial partners. This opportunity window precedes the development of an immune response during the juvenile stage and varies across coral taxa, but may take a few months to years (Little et al. 2004, Abrego et al. 2009b, Puill-Stephan et al. 2012a). Administering a 'probiotic' treatment, which incorporates a community of beneficial symbionts, could allow researchers to control the early 'infection' of coral settlers with select communities, thereby increasing resilience and optimising growth and fitness. As a first step, Damjanovic et al. (2017) demonstrated that a single microbial inoculation of adult corals drove a shift in the microbiome. Similarly, Rosado et al. (2018) showed that a consortium of native and putatively beneficial microorganisms administered as a probiotic to adult corals was able to partially mitigate coral bleaching in a laboratory thermal-stress experiment. Defining the ontogenetic variability in the microbiome and the species-specific life-history window when corals have considerable flexibility to associate with a diverse range of environmentally acquired and potentially stress-tolerant symbionts prior to community specialisation should be a future research priority.

8. AGE AND SIZE AT SEXUAL MATURATION

It can take 3 to 8 yr or more for a coral to reach sexual maturation (Kojis & Quinn 1981, Babcock 1991, dela Cruz & Harrison 2017). Reducing this duration to promote early maturation has many potential restoration applications. Yet, the factors that govern the onset of sexual maturation in corals, and how phenotypically plastic that onset may be, are largely unknown.

8.1. Is sexual maturation determined by age or size?

For most colonial organisms, including scleractinians, a critical-size threshold must be reached to trigger the onset of sexual maturation, beyond which, fecundity increases with size until a colony is fully reproductive (Connell 1973, Loya 1976, Kojis & Quinn 1981, 1985, Harriott 1983, Szmant-Froelich 1985, Wallace 1985, Babcock 1991, Soong & Lang 1992, Hall & Hughes 1996). Only some corals in a population mature at the size threshold (Szmant-Froelich 1985, Babcock 1991, dela Cruz & Harrison 2017), however, and estimates of that size have only been described for a handful of species, ranging widely from 2.3 cm^2 in the brooder *Favia fragum* to 1600 cm^2 in the spawner *Acropora palmata* (Soong & Lang 1992). Soong (1993) identified a significant positive correlation between size at first reproduction and maximum colony size for 7 brooding and spawning Caribbean species, suggesting that larger species generally mature later and at a larger size than smaller ones (MacArthur & Wilson 1967, Szmant-Froelich 1985), although this has yet to be investigated for most species. The onset of sexual maturation is difficult to predict, as it is likely to be influenced by spatio-temporal variation in biological condition (Harvell & Grosberg 1988) and by variation in coral growth rates, which are in turn influenced by many factors, including competition (Rinkevich & Loya 1985, Tanner 1995), light availability (Huston 1985, Lough & Barnes 2000), nutrient profiles and concentrations (Tomascik & Sander 1985, Fabricius 2005), symbiont communities (Jones & Berkelmans 2010), and host genetics (Drury et al. 2017). Consequently, variations in these factors all have the potential to affect the timing of sexual maturation.

Fragmentation and partial-mortality events have the potential to reduce a colony's size below the critical threshold for reproduction. In these cases, the colony becomes small, while the polyps remain 'old', leading Connell (1973) to pose 2 questions: (1) Is sexual maturation in corals determined by polyp age or colony size?; and (2) Will a reduction in colony size result in a regression to a juvenile state? Kojis & Quinn (1981, 1985) experimentally fragmented mature adult *Goniastrea* colonies into various size classes and found that sexual reproduction ceased when the total number of polyps was reduced below 30, even after 2 yr of recovery. However, when they compared reproductive colonies of the same size but different ages, they found that older colonies were more fecund, indicating that age also influences reproductive output. Similarly, Szmant-Froelich (1985) found that fragmenting adult *Orbicella annularis* colonies below 200 cm^2 in surface area reduced or prevented gonad development. Subsequent fragmentation studies of spawning and brooding species found that both colony size and polyp age can influence fecundity (Ward 1995, Smith & Hughes 1999, Zakai et al. 2000, Okubo et al. 2007, Kai & Sakai 2008), and led Graham & van Woesik (2013) to suggest that the reproductive response to fragmentation below the critical-size threshold may be binary and species-specific, where some species maintain gametogenesis while others regress to an immature state. Research over 30 yr has identified at least 7 considerations when predicting whether fragmented corals will reproduce: (1) size of the fragment; (2) age of the fragment; (3) shape of the fragment and location of polyps; (4) mode of polyp budding; (5) timing of fragmentation; (6) duration of fragment isolation; and (7) species (Table 1).

Table 1. Key factors to consider when fragmenting corals for restoration, to maintain the greatest possible reproductive output

Key consideration	Description	Restoration optimisation	References
Size of the fragment	If a coral is fragmented below the minimum-size threshold, the likelihood of regression to a prepubescent state is high and may result in resorption of oocytes	Maintain fragments well above the minimum-size threshold (measured by excluding infertile margins). If not known, select colonies >25 cm in diameter, as most studies to date indicate colonies of this size should be sexually mature	Kojis & Quinn (1985), Szmant-Froelich (1985), Lirman (2000), Zakai et al. (2000), Okubo et al. (2007)
Age of the colony	There may be a minimum age at which a colony can reach sexual maturation. When colonies of the same size but different ages are compared, the older colony may be more fecund	If known, select colonies well above the minimum age of sexual maturation to maximise spawning output. If not known, select colonies >25 cm in diameter, as most studies to date indicate colonies of this size should be sexually mature	Kojis & Quinn (1985)
Shape of the fragment and location of polyps	Colonies exhibit considerable spatial variability in polyp fecundity. Colony margins and axial polyps are often infertile, and downward-facing tissue on branches and vertical surfaces on mounding corals have lower fecundity	Optimise reproductive output by collecting centrally located fragments and fragments with upper-facing surfaces. Limit the creation of new colony margins	Wallace (1985), Soong & Lang (1992), Van Veghel & Bak (1994), Nozawa & Lin (2014)
Mode of polyp budding	Interior polyps newly produced by intratentacular budding were fully fecund in *Favia fragum*, whereas polyps newly produced by extratentacular budding in *Pseudodiploria* spp. were infertile	Anticipate potentially higher reproductive output from fragments of species that bud intratentacularly	Soong & Lang (1992)
Timing of fragmentation	Timing within the gametogenic cycle can influence fecundity post-fragmentation. Fragmentation during early vitellogenesis (i.e. yolk development) has been shown to result in resorption of oocytes	Fragment late in the gametogenic cycle but limit fragmentation in the days immediately prior to spawning to avoid stress-spawning	Okubo et al. (2007)
Duration of fragment isolation	Some species may exhibit 'reproduction adaptation', whereby polyps on fragments that have been isolated for several years (e.g. on individual branches) may become fecund even if the fragment remains below the critical-size threshold	If collecting fragments near the minimum-size threshold, select those that appear to have been isolated for a long duration, with healed and growing margins	Szmant-Froelich (1985)
Species	Some species regress to an immature state when fragmented below the minimum-size threshold (i.e. *Favia chinensis*) and others remain reproductively active (e.g. *Goniastrea aspera* and *Pseudodiploria strigosa*)	If known, select colonies that remain reproductively active post-fragmentation. When fragmenting species that regress, create fragments above the critical-size threshold	Kai & Sakai (2008), Graham & van Woesik (2013)

8.2. Is it possible to artificially accelerate sexual maturation?

Accelerating sexual maturation through the growth and isogenic fusion of microfragments (sensu Page et al. 2018) in a process called 're-skinning' (Forsman et al. 2015) has the potential to reduce generation times and consequently increase coral-recovery rates and restoration outputs. Preliminary results from fused microfragments of *Orbicella faveolata* (Forsman et al. 2015) indicate that sexual maturation may be artificially accelerated by promoting the fusion and growth of the colonies to the critical-size threshold (Page et al. 2018). More research is needed, however, to evaluate the suitability of this technique for other species and growth morphologies. For example, in some massive corals, the fecundity of individual polyps will be influenced not only by colony size (area) but also by tissue depth, which may be limited in re-skinned corals.

9. FEASIBILITY OF LARGE-SCALE RESTORATION

Restoring degraded reefs with sexually propagated corals is being considered or applied on reefs around the world at various spatial scales and with numerous approaches. Comprehensive desktop analyses comparing a multitude of approaches are currently underway to examine the benefits, risks, and feasibility of both influencing the long-term health and survival of corals, and facilitating acclimatisation and adaptation of coral populations at scale (The National Academies of Sciences, Engineering, and Medicine 2019; www.gbrrestoration.org). In Australia, a range of scalable methods are being considered that rely on the sexual propagation of corals, either through the capture and redirection of wild spawn, or from land- and/or sea-based aquaculture production facilities. Preliminary analyses indicate that there are common bottlenecks to achieve cost and scale across all approaches, relating to key biological and ecological attributes of coral reproduction. For example, high *in situ* mortality post-settlement means (1) nursery-reared corals will need to be kept for weeks or months to pass a size-escape threshold, (2) the production numbers required to achieve scale will need to be very large, and (3) the estimated cost per deployed coral surviving to adulthood will be inflated (Omori 2019). The extent to which early growth and survival of corals can be enhanced will materially affect the cost and scale at which sexually produced corals can be feasibly used. Analyses thus far have also clarified that, while extensive effort needs to be applied to technological developments in coral sexual propagation, a significant amount of attention also needs to be directed toward investigating fundamental aspects of ecological benefits and risks, such as quantifying trade-offs in growth and thermal tolerance, and identifying the down-stream effects of spawning corals out of season. This research is required to adequately assess the feasibility of the proposed methods.

10. CONCLUSIONS

The success of coral restoration and adaptation interventions will vary among species, sites, reefs, and regions. Incorporating reef-building species that occupy a variety of ecological niches, encompass a range of reproductive modes, include a suite of morphological or functional forms, and include a diversity of species, will be required to facilitate and maximise recovery rates, with the end goal of restoring and maintaining ecosystem functions.

Based on current knowledge, we suggest that a combination of restoration approaches will deliver the greatest benefit, and that restoration interventions should (1) incorporate sexually reproduced corals across a variety of life-history stages, (2) consider the ecology of the target restoration site (Ladd et al. 2018) and implement deployment methods consistent with local ecological processes, (3) incorporate pre-adapted or stress-hardened coral stock, or incorporate methods that support natural processes of adaptation, (4) protect key ecological functions, (5) conserve sociocultural values, such as those held by Traditional Owners and a diverse range of stakeholders, and (6) be logistically feasible and at a cost point for deployment at large scale. Whether it is feasible to achieve these targets through scaled-up coral restoration remains an active area of investigation (Guest et al. 2014) that will require well-developed and integrated research and development plans (our Table 2).

Overcoming the research challenges outlined here will require an unprecedented level of collaboration across nations, research groups, and public and private sectors. To address fundamental research questions and achieve long-term success, researchers and practitioners working in reef restoration must also draw on expertise from vastly different scientific disciplines such as microbiology, genetics, restoration ecology, aquaculture, materials science, and engi-

Table 2. High-priority knowledge gaps identified in the review and corresponding suggested approaches. Expected outcomes of the research for each section of the review are presented based on current state of knowledge

Areas of research that target key knowledge gaps	Approaches to address knowledge gaps	Expected outcomes
Describing and controlling gametogenic and spawning cycles	• Large experimental systems with fine-scale control over *ex situ* environmental conditions, with and without off-set seasonal and diel cycles • Histological sampling to identify the timing of gametogenesis in the field • Field monitoring of key functional groups (e.g. massive *Porites*) to more accurately identify *in situ* spawning patterns • Development of an integrated on-line system for collecting and synthesizing regional or global spawning observations	• Ability to predict more accurately which species will spawn, where and when • Aquaculture systems that enable manipulation of seasonal and lunar cycles to synchronously spawn corals 'out-of-season' • Ability to adjust diel timing of coral spawning to increase culture efficiencies • Better understanding of the molecular mechanisms and environmental factors underpinning function of endogenous reproductive rhythms in corals • Knowledge to assess the risk of spawning asynchrony in restored corals
Characterization of spawn slicks	• Field monitoring for the presence or absence of slick formation, and coincident collection of environmental data • Remotely sensed detection of spawn slicks • Field sampling for histological and genetic identification of species composition and diversity within slicks, and embryo viability • Field experimentation to contain, collect and transport spawn slicks • Field and lab experiments and modelling to understand and quantify processes (including sperm density and gamete quality) affecting coral fertilization success	• Predictive models to estimate when and where spawn slicks will form • Ability to target slicks to maximize the diversity of species harvested for restoration • Ability to effectively harvest and transport spawn slicks for reef restoration • Knowledge of stocking densities that are adequate to ensure self-sustaining fertilization and larval production
Identification of larval settlement cues and inhibitors	• Laboratory-based biochemical and larval-behaviour assays to identify inducers and inhibitors for a wider range of coral taxa, and define relevant effective doses • Evaluation of the microhabitat and environmental factors, including influence of biofilm succession, and conditioning timing and duration on settlement and post-settlement survival in the lab and field, for a wider range of species	• Identification of cues to induce and improve settlement of a diversity of coral taxa • Set of 'best-practices' for settling a diversity of species (e.g. culture conditions, densities, durations, flow rates, substrate conditioning protocols) • Ability to characterise and identify optimal candidate restoration sites • Ability to induce settlement at specifically targeted locations or optimal 'receiving sites'
Establishing symbioses	• Laboratory and field experiments to build basic knowledge around how (horizontally, vertically or dual mode transmission) and when symbiosis gets established • Genomic techniques to determine uptake and ontogenetic variability in the microbiome from embryo to juvenile • Laboratory inoculation experiments followed by out-planting and time-series sampling to evaluate the feasibility of establishing and maintaining select symbiotic partners • Laboratory experiments to evaluate the impact of stress hardening on embryos and larvae	• Effective uptake and transmission methods to maximize symbiosis success and long-term maintenance • Identification of symbiotic partners that may enhance coral performance in a warming climate • Stress-hardening methods to improve thermal tolerance of embryos and larvae
Overcoming the post-settlement survival bottleneck	• Development of ecologically safe and effective juvenile deployment substrates and efficient methods to deploy • Laboratory choice and no-choice settlement experiments with a suite of shapes and substrate types to identify optimal substrates for post-settlement survival • Field experiments to track post-deployment survival and compare substrate performance across reefs, reef zones and species and under different levels of competition and predation • Field experiments to investigate density-dependent effects of settlement on survival • Laboratory experiments to test the effect of nutrition and probiotic treatments on growth and survival, and evaluate a suite of delivery methods	• Species-specific ability to maximize post-deployment survival and growth • Ecologically effective and cost-efficient substrata for outplanting corals • Nutrition and probiotic profiles, concentrations, and delivery methods that optimize growth and post-settlement survival
Identifying the factors that control the onset of sexual maturity	• Laboratory and field experiments with adult, fragmented, microfragmented, and isogenically fused coral colonies to identify the factors governing the onset of sexual maturation for a diversity of species • Laboratory experiments to determine the factors that promote early maturation and identify what physiological/ecological trade-offs are associated with early maturation (if any)	• More accurate models of population growth and response to restoration for a diversity of species • Ability to shorten generation times by inducing early maturation in selected strains of coral or young, isogenically fused corals
Age and size at sexual maturation	• Temporal field sampling with histological analyses to identify minimum size-thresholds for sexual maturation for a diversity of species • Laboratory experiments to determine the effects of fusion and fission of colonies on reproductive output, including the effects of timing, fragment size, age, etc.	• Ability to optimise fragmentation and other asexual propagation methods to maximise reproductive output
Coral aquaculture research and development	• Development of automated high-throughput aquaculture production • Time series genomics sampling and analysis of batch cultures throughout embryogenesis and larval development (culture genetics) to identify the most successful genotypes and assess the risk of 'lab-adapted' corals on potential performance on reefs	• Ability to propagate corals in large quantities and at low cost • Estimates of the risk of rearing 'laboratory-adapted' corals that may result in maladapted genotypes that have impaired performance on reefs

neering. Key knowledge gaps in the science of coral sexual reproduction are reported in Table 2 and offer a list of high-priority research questions to quickly move the field toward potentially feasible and cost-effective restoration. We emphasise that no approach will be successful without swift and effective efforts to mitigate greenhouse gas emissions. Mitigation must go hand-in-hand with these restoration approaches, as intervention is intended only to temper decline and accelerate natural recovery at more local scales while global efforts take effect to slow the rate of ocean warming and acidification.

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