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Coral propagation: a review of techniques for ornamental trade and reef restoration

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Abstract

Aquaculture of coral offers an alternative to wild harvest for the ornamental trade and shows considerable promise for restoring reefs and preserving biodiversity. Here, we compare advantages and disadvantages of asexually derived fragments versus sexually derived propagules and *in situ* versus *ex situ* nursery phases for the ornamental trade and reef restoration. Asexual propagules, sourced from a donor coral colony that is cut into smaller parts and attached to artificial substrate, are most commonly used. The most suitable corals are typically branching species, although fragments from species with other growth forms can be successful, albeit slower growing. Sexually derived propagules are collected from the wild or from colonies in aquaria during spawning, with an artificial substrate provided for settlement. The timing of spawning is known for many broadcast spawning corals, but opportunities for collection of gametes are generally limited to only once or a few times per year. Brooding species with multiple periods of larval release provide better options for culture of sexually derived propagules. Propagation techniques have developed considerably over the past 20 years, yielding faster growth rates, reduced mortality and reduced detachment from substrates. Simple and cost–effective propagation techniques can be used to restore denuded reefs, preserve endangered species, provide live corals to the international ornamental trade, enable livelihood diversification for coastal communities and provide experimental materials for marine research. This review provides a comprehensive synthesis of recent developments in aquaculture propagation techniques for the purpose of ornamental trade and coral reef restoration, including asexual and sexual propagation, nursery and transplantation stages.

Key words: coral aquaculture, coral fragments, coral propagation, coral spawning, ornamental trade, reef restoration.

Introduction

Coral reefs are the largest living structures built by modular, colonial organisms in the world. Corals are home to incredible biodiversity and are paramount in providing the structural habitat, food sources and settlement cues that many marine organisms depend on to survive and reproduce (Stella *et al.* 2011). The structural complexity of coral reefs is positively associated with biomass and density of fish species (Graham & Nash 2013) and plays a significant role in mitigating the effects of habitat disturbances on the structure of reef fish communities (Emslie *et al.* 2014). Corals (Anthozoa: Cnidaria: Scleractinia) typically represent colonies comprised of many individual polyps. Colonies grow by budding new polyps, a process of modular iteration. Over many generations, a scleractinian coral colony creates a large calcium carbonate skeleton that is characteristic of the taxa. The majority of corals breed sexually by broadcast spawning (Baird *et al.* 2009), and typically colonies of the same species release gametes simultaneously over a period of one to several nights following a full moon, generally in late spring (Babcock *et al.* 1986). Although some corals catch plankton and small fish using nematocysts or trap particulate matter through mucus or

mesenterial filaments, most corals obtain a significant proportion of their energy from zooxanthellae; photosynthetic dinoflagellate algae that live within the corals' tissue.

The ease with which corals can be propagated and maintained in captive environments is largely due to their modular habit, asexual and sexual reproductive mechanisms and minimal feeding requirements. Coral propagation is accessible to a range of aquaculturalists, including aquarists seeking to propagate ornamental species sustainably, large commercial operations and impoverished coastal fishing villages seeking alternative sources of income. Propagation of corals, particularly through asexual reproduction or 'fragging', is a simple process and does not require elaborate equipment or specialised skills. Thus, coral propagation can be easily practiced in developing parts of the world, which are commonly associated with greater amounts of reef degradation as a result of destructive fishing activity and high pollution levels (Hughes *et al.* 2003; Bellwood *et al.* 2004). A nursery phase is commonly used post-settlement or post-fragmentation to allow colonies to grow to a suitable size with reduced competition from fouling organisms and protection from predation (Rinkevich 2000; Epstein *et al.* 2001; Nakamura *et al.* 2011; Guest *et al.* 2014). Following the nursery phase, coral colonies can be transplanted onto denuded reefs (Rinkevich 2000; Boch & Morse 2012; Villanueva *et al.* 2012; Guest *et al.* 2014) or used to supply demand from hobbyists in the live coral trade (Delbeek 2001; Tlusty 2002; Wabnitz *et al.* 2003; Petersen *et al.* 2008; van Os *et al.* 2012; Rhyne *et al.* 2012; Rocha *et al.* 2013a).

Coral propagation methods have numerous environmental and social benefits in comparison to wild collections, including negating anthropogenic impacts, preserving biodiversity, advancing scientific knowledge and improving trade. Trade in hard and soft corals largely comprises harvest from coral reefs and provides revenue for many developing countries. Aquaculture provides an alternative and largely sustainable mechanism for supplying demand of coral species that are highly desired for ornamental trade (Table 1). Moreover, *in situ* aquaculture production has the potential to provide ecological, economic and social benefits to communities (Rhyne *et al.* 2012). Integration of new coral colonies has the potential to repair degraded reef habitats that have been devastated by anthropogenic activity and natural disasters (see Edwards *et al.* 2010 for a thorough examination of reef restoration protocols, strategies and considerations). Restoration plans usually cater to the specific reef habitat and the corals that comprise it (Rinkevich 2000; Table 2). Passive restoration, including management actions that promote natural recovery, must also be in place in order for the process of active reef restoration to be successful (Gomez *et al.* 2011; Rinkevich 2014).

Many coral propagation techniques remain unpublished to protect industry confidentiality, are imbedded online within hobbyist forums, or alternatively, are published in 'grey literature' (e.g. Calfo 2001). Leal *et al.* (2014) provided the first comprehensive review on *ex situ* coral propagation in the primary literature, including quantitative (growth kinetics and volumetric productivity) and qualitative (shape, colouration and natural product content) aspects of coral biology and propagation techniques for consideration in *ex situ* coral aquaculture. The aim of this review is to complement the current primary literature with a comprehensive review on coral aquaculture through a comparison of asexual and sexual propagation techniques for *in situ* and *ex situ* coral culture to supply the ornamental trade and reef restoration efforts. We identify the most common techniques for successful coral propagation, while acknowledging knowledge gaps, challenges and the research required to advance knowledge of the most appropriate propagation techniques.

Table 1 Top ten coral genera imported to the United States as 'aquacultured' or 'maricultured', most of which are propagated in Indonesia. List derived from a Pet Industry Joint Advisory Council PIJAC survey June 2015 of the three largest US importers of corals and does not account for an estimated 1 million domestic 'fraggers' and semicommercial operations within the United States

Genera	Growth type	Common name(s)
1. *Acropora*	Branching	Staghorn coral
2. *Euphyllia*	Phaceloid or flabello-meandroid with fleshy polyps	Hammer coral, frogspawn, torch coral
3. *Montipora*	Plating, branching or encrusting	*Montipora* coral
4. *Caulastrea*	Phaceloid with fleshy polyps	Trumpet coral or candycane coral
5. *Goniopora*	Massive or submassive; hemispherical or irregular; typically with fleshy collumellae	*Goniopora* or flower pot coral
6. *Echinophyllia*	Plating	Chalice coral
7. *Turbinaria*	Encrusting or laminar	Cup coral, disc coral
8. *Hydnophora*	Submassive, encrusting or branching	Horn coral
9. *Pocillopora*	Branching	Cauliflower coral
10. *Stylophora*	Blunt branching or encrusting	*Stylophora* coral or birdsnest coral

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Table 2 Top ten species used in coral reef restoration projects based on an ISI Web of Science all database search for 'reef restoration'. Endangered status based on the IUCN Red List of endangered species: LC = least concern, NT = near threatened and CR = critically endangered. Geographic ranges follow Veron (2000, 2014)

Species	Growth type	Status	Geographic range
1. *Pocillopora damicornis*	Branching	LC	Very wide
2. *Acropora cervicornis*	Cylindrical branching	CR	Moderate
3. *Stylophora pistillata*	Thick branching	NT	Wide
4. *Montipora digitata*	Rapid branching	LC	Narrow
5. *Acropora formosa*	Cylindrical branching	NT	Moderate
6. *Acropora valida*	Branching	LC	Wide
7. *Porites cylindrica*†	Branching	NT	Moderate
8. *Acropora hyacinthus*†	Laterally plating with thin branches	NT	Very wide
9. *Porites rus*†	Laminar, plating, submassive or branching	LC	Moderate
10. *Echinopora lamellosa*†	Thin plating laminar	LC	Wide

†Coral species exhibiting equivalent use in restoration projects.

Asexual propagation

High wave activity and other physical disturbances often fragment colony branches or break portions of colonies in a process known as fragmentation. Fragments have the ability to reattach to a new substratum and grow into new colonies (Tunnicliffe 1981; Smith & Hughes 1999). Fragments similar to those resulting from natural physical disturbances can be produced in land-based culture facilities (*ex situ*) and in the wild on coral reefs (*in situ*) for a range of purposes, including understanding coral biology (Vizel *et al.* 2011; Osinga *et al.* 2012), coral reef restoration (Rinkevich 1995, 2000, 2006, 2008; Jaap 2000; Okubo *et al.* 2005, 2007; Forsman *et al.* 2006; Latypov 2006; Shafir *et al.* 2006b; Lirman *et al.* 2010; Mbije *et al.* 2010; Shaish *et al.* 2010; Bongiorni *et al.* 2011; Boch & Morse 2012), streamlining culture methods for supply of the live coral trade (Delbeek 2001; Soong & Chen 2003), ecotoxicology experiments (Shafir *et al.* 2001, 2003; Vizel *et al.* 2011; Vijayavel & Richmond 2012), drug discovery (Leal *et al.* 2013) and for supplying coral reef aquaria globally (Delbeek 2001; Shafir *et al.* 2001; Tlusty 2002; Shafir & Rinkevich 2013).

Brood stock or donor coral colonies for fragmentation are predominantly sourced from local wild stocks (Bongiorni *et al.* 2011). Although colonies can be fragmented without translocation of donor colonies (Smith & Hughes 1999; Yap & Molina 2003; Lirman *et al.* 2010), frequently whole colonies are removed from the substratum with a hammer and chisel for translocation to the *in situ* or *ex situ* nursery where acclimatisation or acclimation, respectively, takes place prior to fragmentation (Shafir *et al.* 2001; Forsman *et al.* 2006; Shaish *et al.* 2010). Multiple genotypes and multiple fragments per genotype (i.e. genets) of a single species may be harvested to culture replicates of genetically diverse coral colonies (Shaish *et al.* 2010; Osinga *et al.* 2011; Mbije *et al.* 2013; Shafir & Rinkevich 2013). Genotype can have considerable effects on the growth, survival and disease resistance of coral fragments or nubbins (a few polyps or more) of individuals belonging to the same species (Osinga *et al.* 2011, 2012; Shafir & Rinkevich 2013). Genets may be distinguished using a variety of genetic methods, such as the comparison of microsatellite markers and amplified fragment length polymorphisms (AFLP) (Shafir *et al.* 2006a; Amar *et al.* 2008).

Tools, techniques and fragment size

Asexual propagation protocols may involve either the sacrifice of large colonies through pruning of large numbers of small fragments, or alternatively, the pruning of a few small branches from each of many colonies (Rinkevich 1995, 2000). Various tools can be used to fragment different coral growth types (Fig. 1; Table 3). Scleractinian species can be fragmented successfully with the use of wire cutters (Rinkevich 2000; Shafir *et al.* 2001, 2003; Okubo *et al.* 2005, 2007; Vijayavel & Richmond 2012; Shafir & Rinkevich 2013; Fig. 1). Soong and Chen (2003) also obtained high survival rates using pliers to create fragments of *Acropora pulchra* (Brook 1891). Forsman *et al.* (2006) used tin snips, chisels and wire cutters for *Porites lobata* (Dana 1846) and *Porites compressa* (Dana 1846) to fragment various-sized fragments. Osinga *et al.* (2012) described the separation of individual polyps from *Galaxea fascicularis* (Linnaeus 1767) colonies with tweezers. When fragmenting plating coral species such as those in Pectiniidae, the use of a dremel tool fitted with a diamond wheel allows for precise cutting without damage to individual polyps, which may be

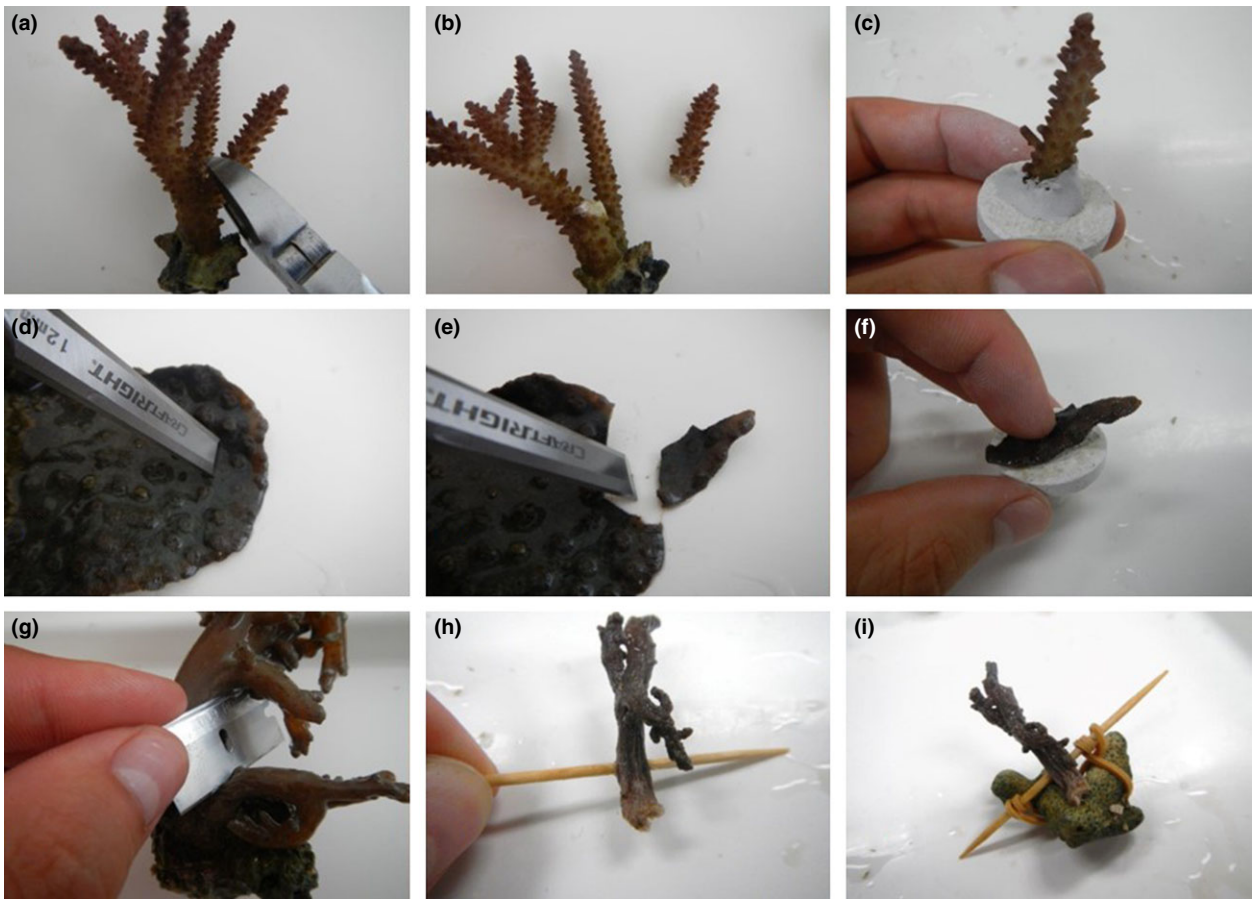

Figure 1 Asexual propagation techniques. (a) tin snips can be used to (b) cut a fragment prior to (c) attachment to an aragocrete plug using epoxy; (d) a chisel is used to chip a fragment (e) from the donor colony (f) which is attached to a plug using glue; (g) a scalpel is used to slice a fragment (h) that is skewered on a toothpick and (i) attached to coral rubble using an elastic band. Images courtesy of Thane A. Militz, James Cook University, Australia.

Table 3 Instrumentation typically used for asexual fragmentation of donor corals

Coral growth type	Tool
Branching	Wire cutters or tin snips
Massive/Submassive	Hammer and chisel
Plating	Dremel tool
Soft	Scalpel

fractured using wire cutters (Borneman & Lowrie 2001). A dremel tool is efficient when fragmenting *Euphyllia* spp., as the thick branches are prone to fracture (JAB, unpublished data). Borneman and Lowrie (2001) suggest the use of a dremel tool for division of massive and submassive growth forms to easily cut through their thick calcium carbonate skeletons. Soft corals, such as *Sarcophyton glaucum* (Quoy & Gaimard 1833), can be fragmented carefully with a scalpel to separate groups of polyps and generate many smaller colonies (Rocha *et al.* 2013b).

Several studies have sought to determine optimal propagation size for survival and growth of coral fragments. Some authors recommend collection of larger fragments to minimise fragment mortality (Bowden-Kerby 1997, 2001; Okubo *et al.* 2005; Forsman *et al.* 2006). Okubo *et al.* (2005) demonstrated high survival rates (100%) of vertically positioned 20 cm tall fragments of *Acropora formosa,* compared with variable survival rates of 5 cm fragments (29.0%). In contrast, Forsman *et al.* (2006) found that by adjusting nursery conditions, survivorship of small fragments could be increased such that there was no significant difference. Fragment size can be vital for successful culture of corals *in situ,* where environmental fluctuations, sedimentation, predation and competition are significant pressures (Epstein *et al.* 2001; Shafir *et al.* 2001, 2003, 2006b; Vijayavel & Richmond 2012; Shafir & Rinkevich 2013). Larger specimens are more suitable for tolerating algal competition and are less vulnerable to predation and sedimentation (Epstein *et al.* 2001; Okubo *et al.* 2005; Latypov 2006; Lirman *et al.* 2010). Lirman *et al.* (2010) observed 87% mortal-

ity of small fragments (2.5 cm long branch tips) of the threatened Caribbean staghorn coral, *Acropora cervicornis* (Lamarck 1816), compared with 13% mortality for larger (3.5 cm long branch tips) fragments under equivalent *in situ* conditions. However, fragments >3.5 cm did not provide additional growth benefits (Lirman *et al.* 2010). The fragment base width to height ratios should be hydrodynamically favourable for branching species (approximately 2–3 height to 1 width), which reduces the probability of fragments detaching from the substrate due to hydrodynamic forces (Shafir & Rinkevich 2013).

In contrast to *in situ* propagation, controlled environments typically provide stable water parameters, low sedimentation, limited predation and controlled competition. Thus, size-specific mortality may be reduced by appropriate captive nursery conditions (Epstein *et al.* 2001; Shafir *et al.* 2001, 2003, 2006b; Forsman *et al.* 2006). The stability of *ex situ* culture allows for successful propagation of coral nubbins that would exhibit significantly higher morality and lower growth rates within *in situ* culture conditions, where growth-limiting factors and mortality-causing agents cannot be easily controlled (Epstein *et al.* 2001; Shafir *et al.* 2001, 2003, 2006b; Vijayavel & Richmond 2012; Shafir & Rinkevich 2013). However, it should be noted that the differential performance of fragments from different genets and species underline the need for fragment size to be chosen based on the aims and culture conditions of respective projects (Rinkevich 2000; Shaish *et al.* 2010; Osinga *et al.* 2011; Mbije *et al.* 2013; Shafir & Rinkevich 2013).

Donor colony mortality, fragment growth and fecundity are also important to consider when selecting fragment size. To reduce stress on donor coral colonies, nubbins or small fragments comprising a minimal number of polyps, can be harvested from the donor, with the number of polyps per fragment depending on polyp size (Epstein *et al.* 2001; Shafir *et al.* 2001, 2003, 2006b; Vijayavel & Richmond 2012; Shafir & Rinkevich 2013). Many nubbins can be collected from small donor colonies (~6.3 cm diameter or more), but pruning more than 10% of donor colony branches may increase stress and subsequent risk of whole colony mortality, while simultaneously reducing fecundity, as observed in *Stylophora pistillata* (see Epstein *et al.* 2001). Lirman *et al.* (2010) demonstrated that collection of small fragments (2.5–3.5 cm) from branch tips of *A. cervicornis* caused no mortality to donor colonies. Following a recovery period, donor branches grew faster than control branches from unfragmented colonies (Lirman *et al.* 2010), suggesting a growth enhancing effect of branch tip fragmentation referred to as pruning vigour.

The fecundity of transplanted coral fragments is relevant to reef restoration efforts because promoting the natural sexual reproduction of coral colonies can improve reef health. Larger fragments (~20 cm long) of *A. formosa* (Dana 1846) and *Acropora hyacinthus* (Dana 1846) showed higher fecundity than smaller transplanted fragments (~5 cm long), as determined by the presence of oocytes in late developmental stages (Okubo *et al.* 2005, 2007). Okubo *et al.* (2007) observed oocyte development of *A. formosa* to be influenced by both fragment size and the developmental stage of oocytes present at the time of fragmentation, with oocytes in the early vitellogenesis (yolk formation) stage typically resorbed. Smaller fragments demonstrated consistent resorption, indicating a reallocation of energy towards growth and survival over reproductive maturity (Okubo *et al.* 2007). With this trade-off in mind, it may be beneficial to transplant larger colonies in coral reef restoration projects to increase the reproductive capacity of denuded reefs more quickly.

Substrate selection

Substrate selection should be tailored to the species being cultured and the suitability of the substrate for ornamental trade or reef restoration. Factors to be considered include the ability of substrate to be cleaned of fouling organisms (Levy *et al.* 2010), propensity to resist settlement and growth of fouling organisms (Tebben *et al.* 2014), source materials available (Ellis & Ellis 2002; Shafir *et al.* 2006a), space available for culture (Ellis & Ellis 2002) and whether or not the fragment will be transplanted onto a denuded reef (Okubo *et al.* 2005; Shaish *et al.* 2010; Boch & Morse 2012; Villanueva *et al.* 2012). Consumer perception of coral substrate should be taken into account when propagating coral to supply the live ornamental trade. Although a large proportion of reef aquarium hobbyists may remove the coral from its substrate, aesthetics and dimensions of the substrates are likely to influence consumer perception (Ellis & Ellis 2002; Tlusty 2002).

Aragocrete is a common fragment substrate generally well received by hobbyists. It is made by mixing equal parts of Portland cement and aragonite sand, which can then be moulded to provide a flat surface area for adhesion of the coral fragment (Fig. 1c). Crustose coralline algae (CCA) readily proliferates on the surfaces of aragocrete, instead of unwanted filamentous algae forms (Delbeek & Sprung 1994), making it more aesthetically pleasing to ornamental enthusiasts (Borneman & Lowrie 2001). 'Live rock' discs are also a suitable substrate for many coral genera (including *Acropora, Euphyllia*, *Porites* and *Turbinaria* (see Ellis & Ellis 2002)), but harvest of live rock can be environmentally destructive (Bruckner 2000). Aragonite can be turned into live rock by seeding pieces in the open ocean to recruit CCA and beneficial bacteria, thus providing an alternative to wild harvest of live rock (Bruckner 2000; Tlusty 2002). Plastic pins, tubing, anchors, stands or rods have also been successfully used as coral fragment substrates (Rinkevich

2000; Latypov 2006; Shaish *et al.* 2010; Osinga *et al.* 2011; Shafir & Rinkevich 2013). Shafir and Rinkevich (2013) attached 3–5 cm coral fragments and nubbins to plastic pins and anchors, with anchors being more suitable for thin branching species due to detachment resistance, and pins being best suited for coral nubbins and massive or encrusting growth forms. Ellis and Ellis (2002) recommend basalt or coral gravel as a substrate for soft coral genera such as *Lemnalia* and *Sarcophyton*, which can be held in place with wooden toothpicks until successful attachment (Fig. 1h). Other viable options exist for soft coral species, with *Sarcophyton* cf. *glaucum* fragments observed to successfully attach to plastic coral stands with rubber bands that can be removed once successful fusion to the substratum is observed (Rocha *et al.* 2013b).

Common coral adhesives include various types of epoxies and cyanoacrylate gels. Epoxy putties are useful because of their strength but cyanoacrylate gels perform better when attaching fragments to smooth surfaces (Fig. 1). Borneman and Lowrie (2001) suggest the use of two part (powder and solvent) surgical bone cement, which they found to be the best performing attachment adhesive, hardening to a density similar to bone within 5 min. Osinga *et al.* (2012) demonstrated that positioning of *G. fasciculari*s fragments within two part epoxy plays a significant role in fusion of developing colonies to their substrate. When the dead skeletal region of a fragment was not completely covered with epoxy, successively developed polyps did not attach to the substrate and instead grew outward supported only by the initial polyp. In contrast, fragments positioned more deeply into the epoxy to completely cover the skeletal region without living tissue, had newly formed polyps that showed consistent attachment to the substrate (Osinga *et al.* 2012). Ensuring that the bases of coral fragments (fragmented surface) are dry before application of glue or epoxy can also increase the effectiveness of attachment procedures (Shafir & Rinkevich 2013).

Rope nurseries can utilise the surface area and coiling force of ropes to hold fragments in place without adhesives. Adhesive-free *in situ* coral nursery techniques can reduce detachment rates and proliferation of biofouling organisms, as well as improve water flux around cultured corals (Levy *et al.* 2010). Similarly, Boch and Morse (2012) found no detachment with coral fragments inserted into adhesive-free Tygon® tubing and zip tied on to pushmounts (masonry cable tie mounting bases) for transplantation.

Fusion of coral fragments to substrates plays an important role in their long term survival. Some experiments have shown significant loss of fragments due to detachment from the substrate, with detachment rates surpassing direct fragment mortality rates in some cases (Shafir *et al.* 2006a; Shaish *et al.* 2008). The risks of detachment can be higher in areas experiencing high wave action, which has led to floating *in situ* nurseries of *Acropora eurystoma* (Klunzinger 1879), *Acropora pharaonis* (Milne Edwards 1960), *Acropora valida* (Dana 1846), *S. pistillata* and *Pocillopora damicornis* fragments that move with wave action and currents, presumably associated with slightly reduced detachment rates of these fragments (Shafir *et al.* 2006a). Shafir *et al.* (2006b) recommended suspending corals 6 m beneath the water surface so that they are subjected to reduced mechanical forces. Soong and Chen (2003) reduced wave action by culturing *A. pulchra* fragments in a semiprotected nursery in Taiwan. They recorded more damage to colonies by mechanical forces at 5 m compared with 10 m, with the former exhibiting more growth attributed to increased light availability. *In situ* propagation of corals in deeper water presents a trade-off between growth and detachment (Soong & Chen 2003). At depth, less light is available, reducing the photosynthetic potential of symbiotic zooxanthellae; hence, the quantity of photosynthates translocated to the coral host and the growth capacity of coral colonies. Additionally, growth of colonies can be reduced by insufficient water turbulence at depth through limitation of the supply of essential nutrients and passive facilitation of metabolic waste export from coral colonies (reviewed in Osinga *et al.* 2011).

Sexual propagation

Sexual propagation protocols have developed considerably over the last 15 years, with successful techniques established for both brooding and broadcast spawning species (Heyward & Negri 1999; Petersen *et al.* 2006; Linden & Rinkevich 2011; Baria *et al.* 2012; Guest *et al.* 2014). Gametes from broadcast spawning corals and brooding corals can be collected *in situ* by positioning non-invasive collection devices around individual colonies (Petersen *et al.* 2006; Horoszowski-Fridman *et al.* 2011). Alternatively, corals can be harvested prior to spawning events and maintained in hatcheries (Petersen *et al.* 2006; Nakamura *et al.* 2011; Boch & Morse 2012). Harvest of *Acropora tenuis* (Dana 1846) gametes from spawning slicks during mass spawning events is a viable collection method if the timing of spawning is known (Omori 2005; Petersen *et al.* 2006; Omori *et al.* 2008) and high fertilisation and survival rates have been achieved *ex situ* for *Acropora* species (>90%) (Willis *et al.* 1997; Epstein *et al.* 2001; Nakamura *et al.* 2011; Villanueva *et al.* 2012; Guest *et al.* 2014). Raymundo and Maypa (2004) found the settlement and early survival rates of *P. damicornis* larvae to be superior under *ex situ* laboratory conditions compared to *in situ* where larvae settled directly onto reef substrate. It is noteworthy that in some geographic locations (e.g. southern Great Barrier Reef, Queensland and high latitude reefs in Western Australia), larvae of *P. damicornis* may be asexually pro-

duced, thus juveniles raised from larvae of this species may have low genetic diversity (e.g. Ayre & Miller 2004; Miller & Ayre 2004).

Fertilisation primarily consists of mixing sperm and eggs in a container with fresh, filtered sea water. For species of *Acropora,* optimal sperm density is in the order of 10^4–10^6 sperm per mL to ensure fertilisation success but minimise polyspermy (Willis *et al.* 1997). Water quality can be maintained by water changes to remove excess sperm once the first cleavage stage is confirmed (Villanueva *et al.* 2012; Fig. 2a). High filtration (e.g. ≤1 μm filtration (Iwao *et al.* 2002; Petersen *et al.* 2006; Guest *et al.* 2014)) and UV treatment (Guest *et al.* 2014) reduce the risk of introducing potential pathogens to developing larvae (Fig. 2e). Before settlement, it may be beneficial to introduce planula larvae (Fig. 2g) to tanks containing zooxanthellae. *Acropora tenuis* larvae introduced to tanks containing large concentrations of zooxanthellae resulted in >90% of larvae incorporating the zooxanthellae to establish the photosynthetic coral/algal holobiont, compared with <1% symbiotic acquisition in settlement tanks (Petersen *et al.* 2008). The sooner zooxanthellae become associated with larvae, the quicker the larvae may be able to utilise the various photosynthates produced by zooxanthellae photosynthesis (Osinga *et al.* 2011).

In contrast to the larvae and juveniles of most broadcast spawning corals, which acquire zooxanthellae from the environment, zooxanthellae are maternally (vertically) transmitted to oocytes in most brooding corals (see Baird *et al.* 2009 for review). Kruger and Schleyer (1998) noted *Pocillopora verrucosa* (Ellis & Solander 1786) oocytes to contain an abundance of zooxanthellae a few days prior to spawning, but also observed oocytes of *P. verrucosa* to be devoid of zooxanthellae 6 days prior to spawning, suggesting potential lunar variability of establishment. A few broadcast spawning genera also have vertical transmission of zooxanthellae, notably *Porites* and *Montipora* (Harrison & Wallace 1990; Baird *et al.* 2009). Due to variability in zooxanthellae transmission modes among coral species, we recommend adoption of zooxanthellae exposure protocols utilised by Petersen *et al.* (2008; as described above) only for broadcast spawning corals that acquire zooxanthellae horizontally (i.e. from the environment). The intraspecific lunar seasonality of this phenomenon should also be considered (Kruger & Schleyer 1998).

Settlement techniques

Settlement occurs when planula larvae find a suitable substrate for attachment and complete metamorphosis. Larvae can be released directly onto degraded reefs for natural settlement (Heyward *et al.* 2002) or settled onto substrates within *ex situ* facilities and *in situ* locations (Iwao *et al.* 2002; Omori 2005; Petersen *et al.* 2006; Omori *et al.* 2008; Horoszowski-Fridman *et al.* 2011; Linden & Rinkevich 2011; Nakamura *et al.* 2011; Baria *et al.* 2012; Villanueva *et al.* 2012; Guest *et al.* 2014). Without the appropriate cues for settlement and metamorphosis, planula larvae may retain their larval state and die (Bishop *et al.* 2006; Gleason & Hofmann 2011). Coral larvae from *Acropora millepora* and other *Acropora* species initiate larval metamorphosis in the presence of a range of species of CCA, particularly *Titanoderma prototypum,* as well as a noncoralline algae, two branching species of coralline algae and the skeleton of *Goniastrea retiformis* (see Morse *et al.* 1988; Heyward & Negri 1999; Harrington *et al.* 2004). Improved settlement rates of planula larvae can therefore be achieved in captive populations by providing appropriate substrates (Fig. 2h).

Providing appropriate settlement substrates can trigger metamorphosis, but different coral species are likely to display variable specificity. Guest *et al.* (2014) conditioned settlement substrata for 3 weeks prior to spawning *A. millepora* in flow-through seawater tanks which contained CCA, thus allowing accumulation of a biofilm containing suitable cues for settlement and metamorphosis of larvae. Water soluble compounds produced by bacterial biofilms attract coral larvae, whereas those released by many species of macroalgae deter larval settlement (reviewed in Birrell *et al.* 2008; Gleason & Hofmann 2011). Conditioning or seeding of artificial substrates on coral reefs prior to introduction of larvae can increase settlement of *Acropora* spp. larvae, but care should be taken to prevent contamination by removal of any unwanted algae or other biofouling organisms before introduction of the substrates to hatchery systems (Harrison & Wallace 1990; Omori & Iwao 2009; Boch & Morse 2012).

The amount of time elapsed before settlement competence varies between species (Table 4). Larvae of brooding corals are typically able to settle within hours (e.g. *Pocillopora, Seriatopora, Stylophora, Isopora*), whereas larvae of broadcast spawning corals typically require 3–4 days of planktonic development before becoming competent to settle (e.g. *Acropora, Montipora,* faviids including *Favia, Platygyra, Goniastrea*) (Babcock & Heyward 1986; Heyward *et al.* 1987; Harrison & Wallace 1990; Heyward & Negri 1999; Isomura & Nishihira 2001; Miller & Mundy 2003; Nozawa & Harrison 2005; Wilson & Harrison 2005; Nozawa *et al.* 2006; Petersen *et al.* 2006; Gilmour *et al.* 2009; Gleason & Hofmann 2011). Larvae of some spawning species may remain competent to settle for 195–244 days, although rates of mortality increase progressively after 100 days (Graham *et al.* 2008). Boch and Morse (2012) used a settlement competency check (described as metamorphosis assays by Heyward and Negri (1999)) by placing 10 larvae in each of 12 culture plates with 10 mL of seawater and a 3 mm chip of CCA. They recommended introduction of larvae to settlement tanks once ≥50% settlement

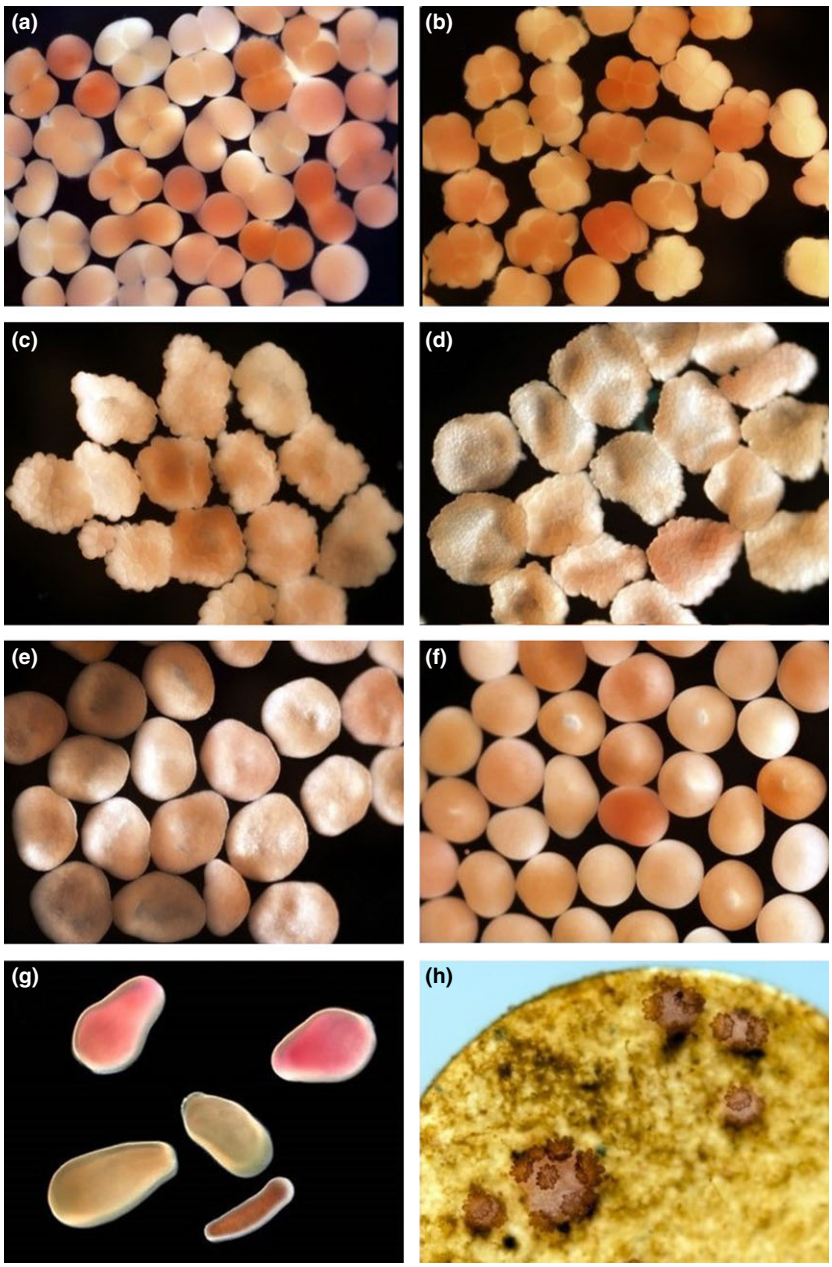

Figure 2 Embryogenesis of *Acropora tenuis*. (a) cleavage; (b) multicellular; (c) blastula flattens; (d) late blastula; (e) early gastrula; (f) late gastrula with oral pore; (g) planktonic larvae; (h) sexually derived recruits on an aragocrete plug. Images courtesy of BLW and E. Matson (2h).

competency is observed. Larvae of broadcast spawning species can demonstrate settlement competency as early as 2–3 days postfertilisation (Heyward *et al.* 1987; Harrison & Wallace 1990; Miller & Mundy 2003), while others take 4–9 days postfertilisation (Babcock & Heyward 1986; Heyward & Negri 1999). Petersen *et al.* (2006) found considerable differences in duration before settlement competency between brooders and broadcast spawners, with larval settlement of the brooders *Favia fragum* (Esper, 1797) and *Agaricia humilis* (Verrill, 1901) occurring within 24 h, whereas settlement of the broadcast spawner, *A. tenuis*, occurred between 1–6 days. Larvae produced by brooding pocilloporid corals, *P. damicornis*, *Seriatopora hystrix* (Dana 1846) and *S. pistillata* are ready to settle 12 h post-release, with all larvae settled within 96 h (Isomura & Nishihira 2001). Variance in time before settlement can occur even between species of the same genus, which suggests aquaculturalists need to adapt settlement protocols

Table 4 Known settlement inducers for coral species and their associated settlement competency periods

Coral species	Settlement inducer	Settlement competence	Reference
Acropora valida	Coral rubble with CCA	7 days postfertilisation	Villanueva *et al.* (2012)
Acropora palmata	Hym-248 neuroeptide	100% completed metamorphosis by 6–7 days postfertilisation	Erwin and Szmant (2010)
Acropora tenuis	Hym-248 neuroeptide	Not disclosed	Harrington *et al.* (2004) Iwao *et al.* (2002)
	TBP	Within 24 h	Tebben *et al.* (2015)
Acropora nasuta	Hym-248 neuroeptide	Not disclosed	Iwao *et al.* (2002)
Acropora millepora	8 species of CCA	>80% completed	Harrington *et al.* (2004)
	400 μm holes in substrate	Metamorphosis 7–9 days postfertilisation	Heyward and Negri (1999)
	Live CCA	3 days postfertilisation	Whalan *et al.* (2015)
	TBP	Within 24 h	Tebben *et al.* (2015)
Acropora surculosa	Live CCA	Within 24 h	Tebben *et al.* (2015)
	TBP	Within 24 h	Tebben *et al.* (2015)
Acropora globiceps	Live CCA	Within 24 h	Tebben *et al.* (2015)
	TBP	Within 24 h	Tebben *et al.* (2015)
Ctenactis crassa	400 μm holes in substrate	Within 24 h	Whalan *et al.* (2015)
	Live CCA	Within 24 h	Whalan *et al.* (2015)
Lepastrea purpurea	TBP	11 days postfertilisation	Tebben *et al.* (2015)
Montipora hispida	TBP	Within 24 h	Tebben *et al.* (2015)
Pseudosiderastrea tayamai	TBP	Within 24 h	Tebben *et al.* (2015)

CCA, crustose coralline algae; Tetrabromopryrrole (TBP): a bacterial isolate and metabolite associated with *Pseudoalteromonas* bacteria.

according to the specific culture species (Gleason & Hofmann 2011; Table 4). Gilmour *et al.* (2009) note the ambiguity present between documented precompetency periods of larvae. Some studies consider this period to be defined as the point at which larvae have completely metamorphosed into a primary polyp, while others consider the precompetency period to end when larvae attach to the substratum and begin metamorphosis (Gilmour *et al.* 2009). How authors measure the precompetency period should be considered when aiming to develop settlement protocols for a given species.

As described for asexual propagation, it is important to choose a settlement substrate that suits the needs of the project (e.g. reef restoration) and of the cultured species. When settling sexual recruits for reef restoration, Linden and Rinkevich (2011) advocate novel substrate types that are attractive to coral larvae (high surface area), recyclable and replaceable, such as settlement onto terracotta tiles (Harrington *et al.* 2004). Live rock rubble with CCA can also serve as a settlement inducer in *Acropora* spp. (see Villanueva *et al.* 2012). Unglazed ceramic tiles are commonly utilised because they readily foster successful settlement and fusion of scleractinian corals (Raymundo & Maypa 2004; Petersen *et al.* 2005a,b, 2006; Nozawa 2008; Nakamura *et al.* 2011). Some tiles are modified to provide additional surface area for attachment, such as engraving parallel grooves (Petersen *et al.* 2006). To accommodate reef restoration effort, Omori and Iwao (2009) used 'coral pegs' which were composed of a plastic shaft and settlement head made of cement and quartz sand. The coral pegs were designed for easy transplantation onto reefs, following successful recruitment of *A. tenuis* larvae. Guest *et al.* (2014) used a similar substrate consisting of a size 10 wall plug fitted with a cylindrical cement head, providing a settlement substrate that was cost–effective and suitable for *A. millepora*. Similarly, Boch and Morse (2012) used ocean conditioned pushmounts for simple transplantation of *A. hyacinthus* colonies once they grew to an appropriate size.

High concentrations of larvae introduced to settlement substrates may promote fusion. Fusion is the process in which two or more adjacent coral colonies of the same species begin to grow together, sharing resources (Buss 1982; Rinkevich & Weissman 1992; Raymundo & Maypa 2004; Puill-Stephan *et al.* 2012a). Fusion is more likely to occur when coral spat occur in high densities on a settlement substrate. Raymundo and Maypa (2004) utilised fusion to reduce size-specific mortality of juvenile coral colonies, finding reduced morality in colonies <8 months old. Based on the work of Raymundo and Maypa (2004), Boch and Morse (2012) suggest that higher survival rates of juveniles could be achieved indirectly by introduction of a higher density than one planula larvae L^{-1} to settlement substrates. Villanueva *et al.* (2012) did not intend to determine the effects of fusion, but used larval concentrations of 250–300 planula larvae L^{-1} of *A. valida*, which resulted in survivorship of 67.5%, 6 months post-transplantation. Problems with excessive recruitment were highlighted by

Linden and Rinkevich (2011), who remarked that the difficulty faced in previous research with reductions in spat viability and growth rates could be attributed to intraspecific competition (Okamoto *et al.* 2005; Petersen *et al.* 2005a; Nozawa 2008; Omori & Iwao 2009). Puill-Stephan *et al.* (2012b) showed that the fate of fused juveniles depends on the relatedness of larvae, with fusions between nonsiblings resulting in rejection within 3 months. 'Excessive' recruitment prompted Linden and Rinkevich (2011) to utilise a novel technique that incorporated settlement onto double sided matte paper glued within the base and lids of petri dishes. This allowed for individual spat to be removed and glued separately onto plastic pin mounts to be transferred to an *in situ* coral nursery. This method exhibited very high attachment (>95%) and survival (80%) after 1 month by the brooded *S. pistillata* recruits used, 89% of which were alive after 4 months within caged mid-water *in situ* nurseries (Linden & Rinkevich 2011). The success of this technique does not necessarily discredit the utilisation of fusion of coral spat, which could still prove to be viable for increasing survival of juvenile colonies. However, it would be necessary to limit opportunities for fusion to half- or full-sibling larvae to optimise culture techniques.

Water flow, aeration and light can potentially impact successful settlement of sexual recruits. When introducing larvae of *Acropora* spp. (broadcast spawners) to settlement substrates, it is common for flow to be suspended or turned off for 24 h (Nakamura *et al.* 2011; Boch & Morse 2012; Villanueva *et al.* 2012; Guest *et al.* 2014). After this period, gentle flow (1 L s^{-1} in 1000 L of seawater) can be restored to remove any lysing larvae from the settlement tanks (Boch & Morse 2012). Instead of gentle flow, Villanueva *et al.* (2012) gently aerated settlement containers containing *A. valida* larvae as part of the settlement procedure. Similarly, Guest *et al.* (2014) also provided aeration during settlement of *A. millepora* larvae. Previous research recommends low flow-through systems with filters over standpipes or the application of daily (≥50%) water changes up until the desired recruitment of juveniles is achieved, often between 4 and 8 days postfertilisation for broadcast spawning species (Nakamura *et al.* 2011; Boch & Morse 2012; Villanueva *et al.* 2012; Guest *et al.* 2014). Linden and Rinkevich (2011) eliminated direct flow exposure by inserting brooded *S. pistillata* larvae into seawater filled petri dishes, which they housed in a flow-through seawater table to maintain thermal regulation. Two 48 h periods (total 4 days) were allotted for settlement of larvae, with the observed average settlement and survival rates providing a high yield of recruited juveniles, which demonstrates that aeration may not be a critical procedure during settlement (Linden & Rinkevich 2011).

An appropriate light regime impacts behaviour and settlement of coral larvae. Higher survival rates of pocilloporid larvae occur under light as opposed to dark conditions (Isomura & Nishihira 2001). Gleason and Hofmann (2011) highlight a dilemma faced between achieving adequate levels of photosynthetically active radiation (PAR, 400–700 nm) to support settlement and growth to adulthood and avoiding excessive intensities of ultraviolet radiation (UVR, 280–400 nm) that are often associated with high amounts of PAR. It could be argued that the source of the light largely determines how broad the emitted spectra are, and if in fact these light sources emit UVR (Wijgerde *et al.* 2012; Rocha *et al.* 2013a). Light emitting diodes (LED) are known for their very narrow spectral emissions and therefore can virtually eliminate coral larvae exposure to UVR, while simultaneously providing the high irradiance required by many species at optimal wavelengths for zooxanthellae photosynthesis when cultured *ex situ* (Kinzie *et al.* 1984; Kuhl *et al.* 1995; Schlacher *et al.* 2007; Wijgerde *et al.* 2012; Rocha *et al.* 2013a).

The nursery phase

The nursery phase is an integral part of the 'gardening concept' termed by Epstein *et al.* (2001) and Rinkevich (1995, 2000, 2005), which describes the phase of growth and maintenance of corals either *in situ* or *ex situ* before they are transplanted onto denuded reefs or available for sale in the ornamental trade (Fig. 3). The nursery phase allows for rapid growth of specimens under ideal conditions and allows asexual propagules to recover from the trauma of fragmentation by growing tissue over their exposed skeletons. Lirman *et al.* (2010) found that growth of *A. cervicornis* fragments within an *in situ* nursery exceeded that of wild colonies in the same region. Baria *et al.* (2012) also noted higher growth in sexually propagated colonies of *A. millepora* (especially gravid colonies) housed for a longer duration in the nursery compared with transplanted individuals. Asexual and sexual propagules must reach a size at which their vulnerability and subsequent mortality from sedimentation, algal competition and predation can be reduced. The first month of the nursery period is vital in influencing the number of detached or dead coral fragments, because any procedural deficiencies or errors in the fragmentation process are most likely to become apparent before strong fusion of corals to their substrata (Shafir *et al.* 2006a). The size of propagated colonies is not only important for reef restoration endeavours, but also could reduce transport mortality through the ornamental supply chain (Wabnitz *et al.* 2003). Healthy specimens are likely to display the most attractive colouration, increasing their demand by distributors and hobbyists (Delbeek 2001; Ellis & Ellis 2002).

The nursery phase of coral propagation can be conducted exclusively *in situ*, *ex situ* or a combination of

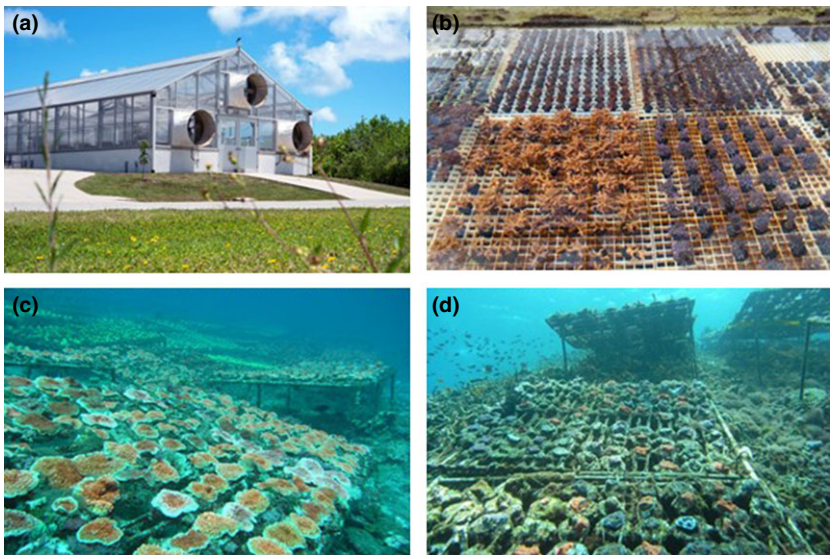

Figure 3 The nursery phase. (a, b) growth and maintenance of corals *ex situ* (courtesy of Oceans, Reefs & Aquariums, USA); (c, d) *in situ* culture before corals are transplanted onto denuded reefs or traded (courtesy of Quality Marine, USA).

both (Fig. 3; Table 5). *In situ* nursery phases rely on the selected habitat to foster coral growth, therefore suitable locations must be chosen carefully. In addition to abiotic influences, such as sedimentation, coral colonies grown *in situ* are exposed to other organisms in those habitats, which can have potentially negative effects on colony growth and mortality. Algal competition and predation must be addressed to prevent the inhibition of growth and maturation of cultured coral colonies. Omori *et al.* (2008) and Omori (2005) nursed *A. tenuis* colonies entirely *in situ* and protected them from predation by enclosure within plastic cages. They also reduced algal competition through the coculture of *Trochus niloticus* (Linnaeus 1767), gastropods that are natural grazers on macroalgae, diatoms and other biofouling organisms such as tunicates. Positioning of juvenile colonies in areas of high flow can also reduce the proliferation of algae and accumulation of sediments that negatively affect coral health (Omori 2005; Latypov 2006).

Table 5 Advantages and disadvantages of *in situ* and *ex situ* coral propagation

In situ propagation
• Typically less expensive (e.g. no light or feed input)
• Exposure to uncontrolled biotic (e.g. predation) and abiotic (e.g. sedimentation) variables
• Colony size restrictions
Ex situ propagation
• High overhead costs (e.g. electric)
• Highly controlled biotic and abiotic environment†
• No colony size restrictions

†While *ex situ* environments are typically highly controlled, potential risks may include power failure, rapid changes in water parameters and disease outbreaks.

In situ nurseries can typically be constructed at low costs in various areas like shallow sand beds, using simple materials such as cinder blocks, cement platforms and PVC frames (Lirman *et al.* 2010). Shafir *et al.* (2006a) also demonstrated cost–effective 'gardening' of colonies in a floating coral nursery with plastic nets suspended 6 m from the ocean surface, held together by PVC framing. Shaish *et al.* (2008) tested for differential effectiveness between fixed and floating coral nurseries. These nurseries contained seven coral species from multiple genets with different growth forms (branching, submassive, leaf-like). Trays were submerged 2 m below the surface in a sheltered lagoon, and both showed high survivorship (>85% and greatest in branching growth forms) and low detachment rates over 1 year (majority of fragments ready for transplantation) with only monthly maintenance. However, they noted that the leg-fixed nursery sustained less damage from strong currents, subsequently requiring less labour for maintenance (Shaish *et al.* 2008). Similar nursery structures have yielded positive results at low costs to researchers for *in situ* coral gardening (Mbije *et al.* 2010, 2013).

The economic viability of coral nursery operations is a serious consideration, regardless of the project goals. To make coral propagation commercially viable, a balance must be established between achieving maximum survivorship with limited operational costs. The nursery period for propagated corals should not exceed what is necessary for each species for the given application (Shaish *et al.* 2008). *Ex situ* nurseries can be advantageous to aquaculturalists by

providing very stable conditions (e.g. no turbidity associated with harsh weather). The stability of water flow, water parameters, light intensity, biofoulant management and feeding regimes are a few of the many factors that can foster high growth rates and survivability when propagating corals.

Feeding

Ex situ nursery systems can consistently provide nutritional supplementation to juvenile or fragmented coral colonies through the addition of live or manufactured feeds. The time period necessary for nubbins and sexually propagated corals to reach a size suitable for sale, transfer to an *in situ* nursery or for transplantation onto a denuded reef can be shortened by enhancing colony growth rates. As no corals are documented to exhibit complete autotrophy, heterotrophy provides essential organic nutrients necessary for coral growth and development (Osinga *et al.* 2011). Organic food sources such as *Artemia* nauplii can provide the coral-zooxanthellae holobiont with nitrogen, carbon and phosphorous in a ratio which suits high photosynthetic activity and subsequent coral growth under proper light conditions (see Houlbrèque & Ferrier-Pagès 2009; Osinga *et al.* 2011). Therefore, regular feeding can potentially reduce the duration spent at fragile initial life stages (Petersen *et al.* 2008). Experiments comparing growth rate enhancement from regular feedings on newly settled primary polyps of *F. fragum* (brooder) and *A. tenuis* (broadcast spawner) showed daily feeding of *Artemia salina* (Linnaeus, 1758) nauplii significantly increased the growth of *A. tenuis* juveniles over 5 months (Petersen *et al.* 2008). Additionally, mean survival rate of *A. tenuis* under all *Artemia* treatments was higher than the control. *Artemia* nauplii provide an inexpensive way to significantly increase growth of sexual recruits in *ex situ* coral aquaculture (Petersen *et al.* 2008; Toh *et al.* 2014).

Feeding *Artemia* nauplii to larval stages of many cultured organisms is a common practice, with *Artemia* cysts readily available and easy to culture. However, sustainability concerns do exist because these cysts are harvested from the wild. There is potential for the utilisation of alternate sustainable live feeds; Osinga *et al.* (2012) described enhanced growth of *P. damicornis* fed the rotifer *Branchionis* sp. (Pallas 1766), and the marine diatom *Tetraselmis suecica* (Butcher 1959), although growth rates were lower than those fed *Artemia* nauplii. The enrichment of *A. salina* and *Branchionis* sp. is already a common practice in the aquaculture industry to provide additional nutrients to larval organisms (Conceição *et al.* 2010). Alternatively, engineered coral food, for example powdered plankton has been used to successfully supplement the diets of coral juveniles (C. Alvarez Roa, personal communication). Whether or not enrichments provide considerable gains in coral growth remains to be explored.

Light

The supply of sufficient photons of wavelengths between 400 and 700 nm is important for maintaining coral health and achieving maximum growth (Osinga *et al.* 2011). During *in situ* nursery phases, the supply of light should typically not be an issue if corals are cultured at an appropriate depth that suits the organism. When propagating corals *ex situ*, artificial light is generally necessary to support coral health and growth. Also, the growth enhancement achieved by the addition of feeds during *ex situ* nursery phases cannot be maximised without ample light supply (Osinga *et al.* 2011). The light demands of coral species are variable, and care should be taken to avoid the supply of excessive light intensity to the zooxanthellae symbionts. An excess of photons can result in photoinhibition, or the shrinking of chloroplasts, which subsequently lowers the photosynthetic capacity of zooxanthellae. Nakamura *et al.* (2011) aligned light intensity in an *ex situ* nursery with natural light intensity of the intended transplantation site. This procedure could potentially lower the occurrence of photoinhibition and general stress on corals acclimatising to the transplantation site.

Not all photons equally promote coral growth. Kinzie *et al.* (1984) noted the association of the primary photosynthetic pigment chlorophyll a, with blue light (430–495 nm) absorption. When examining the growth performance of *Acropora solitaryensis* Veron & Wallace, 1984 grown *ex situ* under four metal halide treatments (150 W bulbs with Kelvin ratings of 20 000, 14 000, 10 000 and 5000 K), Schlacher *et al.* (2007) found the highest growth rate under 20 000 and 14 000 K bulbs which contained more blue light than the other treatments. Not only does blue light appear to enhance the growth and survivability of stony corals, but red light (~630–690 nm used) may repress the photophysiology of scleractinian corals as observed in *S. pistillata* (see Wijgerde *et al.* 2014). It is important to note that emission spectra and irradiance are variable between different brands of bulbs advertised with the same colour temperature.

Practical sources of light provision include metal halide, T5 high output fluorescent, LED (light emitting diode) and light emitting plasma (LEP). LEP and LED light sources are cost–effective because they use less power to achieve the same irradiance as other light sources (T5 and metal halide) and thus can support the sustainability and viability of *ex situ* coral propagation (Rocha *et al.* 2013a). Wijgerde *et al.* (2012) tested the variable effectiveness of LEP and LED light sources at variable irradiance on the growth of *G. fascicularis*. They found both light sources to

be suitable for coral growth, but the LEP lighting yielded higher growth at the highest irradiance treatments (125–150 and 275–325 μmol m^{-2} s^{-1}). This may be attributed to the broad emission bandwidth of LEP modules compared with the narrow bandwidths emitted by the three colours of LEDs used (white, blue and royal blue). However, Rocha *et al.* (2013a) found slightly higher growth with blue LED lighting compared with LEP lighting for *A. formosa* and *S. pistillata* fragments. They assert the importance of more research in determining the suitability of LEP and LED lighting in the culture of more species of scleractinian corals. The utilisation of a larger variety of LEDs within LED modules could potentially increase performance. Additionally, individual LEDs can be easily retrofitted with optics which focus the light into cones of emittance (e.g. 60° optics). This is common in the aquarium industry and can increase the efficiency of LED lighting applications by not 'spilling' photons away from where corals are located.

Biolfoulants and disease

Fouling is the accumulation of microorganisms and macroorganisms on immersed hard substrata. The interaction between corals and fouling organisms, particularly filamentous algae, is generally detrimental for the health of adult corals and settlement of coral larvae (Box & Mumby 2007; Linares *et al.* 2012; Tebben *et al.* 2014). The addition of natural biocontrols in conjunction with manual removal of biofouling organisms reduces competition faced by coral recruits on their respective substrates. Antifouling paint can also reduce fouling coverage and cleaning procedures (Shafir *et al.* 2009). Nakamura *et al.* (2011) added herbivorous sea snails (*T. niloticus* and *Lunella granulata* (Gmelin 1791)) and juvenile fish (*Siganus spinus* (Linnaeus 1758) and *Acanthurus triostegus* (Linnaeus, 1758)) that consume macroalgae and *Chaetodon kleinii* (Bloch 1790) which eats anemones, to their nursery tanks to prevent the inhibition of juvenile coral growth. Juvenile *Siganus* spp. are suitable for small coral colonies, which they can clean without adverse effects. Similarly, Toh *et al.* (2013) used urchins, *Salmacis sphaeroides* (Linnaeus 1758) and sea snails, *Trochus maculatus* (Linneaeus 1758) to improve the efficiency of *ex situ* nursery phase. Additionally, these biocontrols reduced labour expenditure from manual removal of unwanted organisms (Forsman *et al.* 2006; Nakamura *et al.* 2011; Toh *et al.* 2013). Care should be taken in the selection of grazing species because some species can damage smaller coral fragments (Forsman *et al.* 2006).

Disease outbreaks result in coral loss, changes to community structure and associated species diversity. Corals are susceptible to numerous infectious disease agents including bacterial and fungal pathogens as well as parasites (Willis *et al.* 2004; Harvell *et al.* 2007; Bourne *et al.* 2008, 2015). The study of coral disease is in its infancy and while numerous syndromes have been documented, the causative agents have not been identified, and in some cases, disease is thought to be caused by a consortium of pathogens. In the authors' experience, coloured band diseases caused by ciliates are frequently observed in *ex situ* larval and juvenile cultures (BLW, unpublished data). Boring ciliate infections tend to exhibit a speckled black, brown or dark green band at the tissue–skeleton interface and have been documented in a wide range of coral families (Beeden *et al.* 2008; Bourne *et al.* 2008). There are no current strategies for dealing with disease outbreaks other than filtering to <1micron and UV sterilizing the water supply. The addition of natural biocontrols, such as cleaner organisms, could potentially aid in reducing infectious agents (Militz & Hutson 2015) although this has not been quantified for coral pathogens and parasites.

Transplantation

Transplantation enhances reef resilience by directly providing more total coral colonies and subsequently increasing the reproductive capacity of these populations (Horoszowski-Fridman *et al.* 2011). Local coral reef rehabilitation in key locations may result in a gradual increase in species diversity over time (Nakamura *et al.* 2011). Transplantation sites should be chosen strategically by targeting areas with suitable environmental conditions for the proliferation of transplant species (Nakamura *et al.* 2011). A suitable substratum should be stable, and modification may be necessary to provide stability for transplanted colonies. Transplantation should occur in areas with suitable depth and water currents (Suzuki *et al.* 2008). Furthermore, seasonal transplant survival rates indicate that highest survival rates are likely to occur during seasons with lower temperature fluctuations, so avoiding transplantation during the hottest temperatures of the year is advantageous (Okubo *et al.* 2005; Edwards *et al.* 2010; Villanueva *et al.* 2012). The diversity and abundance of corallivores in potential transplant sites should also be considered. Reef restoration efforts focused on restoring a hypothetical denuded reef infested with *Drupella* spp. or *Acanthaster planci* (Linnaeus 1758) would be an inefficient use of the finite resources available for any given reef restoration project. Cages or other protective devices can be used to reduce predation from some corallivores and incidental damage from larger grazing herbivores (Baria *et al.* 2010; Linden & Rinkevich 2011; Nakamura *et al.* 2011), but routine maintenance is required to remove algae and other fouling organisms from these structures. Therefore, it may be more beneficial to allot labour and material expenses towards the determination of suitable sites and the transplantation of more coral

colonies to these sites, thus offsetting the impact of partial colony losses from predation or grazing.

Polyculture

Coral can be cultured in combination with other aquaculture species to promote coral growth and bioremediation. Shafir *et al.* (2006a) showed a significant increase in growth of branching coral fragments (*S. pistillata, P. damicornis, A. pharaonis, Acropora eurystom and A. valida*) cultured adjacent (10 m) to sea caged gilthead seabream, *Sparus aurata* (Linnaeus 1758). The authors attributed the added growth to nutrients in the form of dissolved organic matter produced from the wastes of the cultured sea bream. Similarly, adult corals are known to feed on suspended particulate matter (Anthony 1999), and *Heteroxenia fucescens* (lecithotrophic, nonfeeding and nonzooxanthellae soft coral) planula larvae were observed to absorb significant quantities of nonpolar amino acids (Ben-David-Zaslow & Benayahu 2000), suggesting that larval metabolism could potentially benefit from uptake of dissolved organic matter (Gleason & Hofmann 2011). The potential exists for future research to examine the benefits of dissolved organic matter enrichment for both sexually and asexually derived corals to enhance growth.

Further considerations

Coral propagation represents one of few economic opportunities for sustainable livelihood diversification in islander communities. Asexual coral propagation can cater to the poor and to all genders (Salayo *et al.* 2012), enabling communities to actively participate in ornamental trade or reef restoration. In turn, these practices can restore tourism to proximal reefs, increase biodiversity and provide more local food sources. The National Oceanic and Atmospheric Administration (NOAA) published a workshop report (2010) examining international guidelines for environmentally friendly mariculture (*in situ*) of stony corals, in which they describe that Indonesian regulations require ten per cent of corals cultured in Indonesia be used in reef restoration efforts. Refining government programmes to best direct these restoration efforts could further improve their effectiveness. It is critically important for a balance to be maintained between *ex situ* and *in situ* production in regions such as Indonesia, which exports the majority of aquacultured coral (Table 1). If *ex situ* propagation becomes dominant in these areas, the economic incentive to maintain high coastal water quality (e.g. limit pollution) is likely to be reduced. Furthermore, the CITES Resolution Conference 16.6 suggests that this shift may favour *ex situ* over *in situ* propagation would also reduce revenue in the rural communities that depend on these natural resources.

Sexual propagation of corals maintains genetic heterogeneity for reef restoration and limits damage to rare or endangered parent colonies that may otherwise have been fragmented for propagation. Maintaining genetic heterogeneity can reduce the accumulation of deleterious alleles within small populations and potentially improve the efficacy of reef restoration efforts. Moreover, larvae can be transported between aquaculture facilities to provide sexual recruits for coral propagation facilities worldwide (Petersen *et al.* 2005c). Although cost analysis suggests asexual propagation methodologies are currently more cost–effective means of coral propagation (Villanueva *et al.* 2012), refinement of sexual propagation and nursery techniques could see this change in the future. The inherent differential performance between coral genotypes has great potential to be utilised by aquaculturalists and conservationists alike. Advantageous phenotypes such as enhanced growth rate, disease resistance, thermal tolerance and general survivorship can be artificially selected in breeding programmes aimed to enhance the robustness and survival of corals produced for the ornamental trade in the future. van Oppen *et al.* (2015) include selective breeding in their proposition to assist the natural evolutionary process of corals to cope with the changing temperature and ocean acidification. Although this concept is in its infancy, there exists a considerable potential to enhance survivability of future coral generations.

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