



## Effects of sediments on the reproductive cycle of corals

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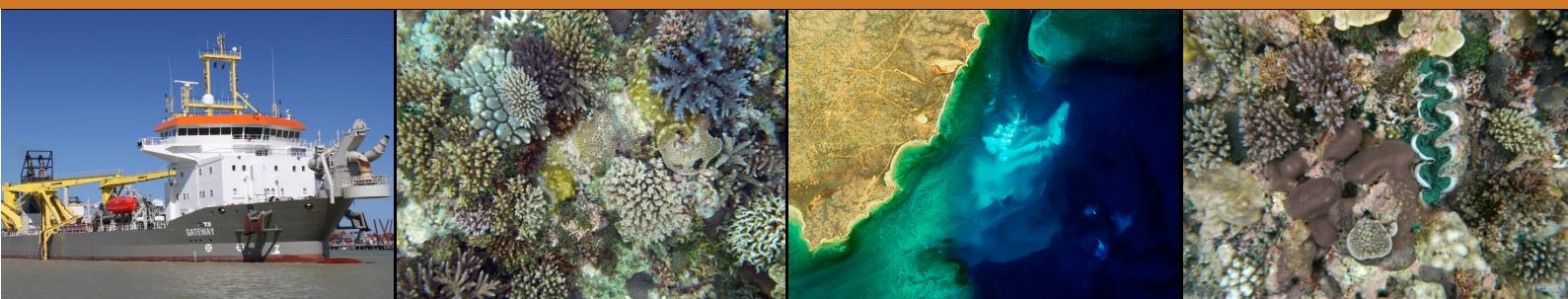
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## WAMSI Dredging Science Node

Theme 7 Report

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## **WAMSI Dredging Science Node**

The WAMSI Dredging Science Node is a strategic research initiative that evolved in response to uncertainties in the environmental impact assessment and management of large-scale dredging operations and coastal infrastructure developments. Its goal is to enhance capacity within government and the private sector to predict and manage the environmental impacts of dredging in Western Australia, delivered through a combination of reviews, field studies, laboratory experimentation, relationship testing and development of standardised protocols and guidance for impact prediction, monitoring and management.

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The \$20 million Dredging Science Node is delivering one of the largest single issue environmental research programs in Australia. This applied research is funded by **Woodside Energy, Chevron Australia, BHP Billiton and the WAMSI Partners** and designed to provide a significant and meaningful improvement in the certainty around the effects, and management, of dredging operations in Western Australia. Although focussed on port and coastal development in Western Australia, the outputs will also be broadly applicable across Australia and globally.

This remarkable **collaboration between industry, government and research** extends beyond the classical funder-provider model. End-users of science in regulator and conservation agencies, and consultant and industry groups are actively involved in the governance of the node, to ensure ongoing focus on applicable science and converting the outputs into fit-for-purpose and usable products. The governance structure includes clear delineation between end-user focussed scoping and the arms-length research activity to ensure it is independent, unbiased and defensible.

And critically, the trusted across-sector collaboration developed through the WAMSI model has allowed the sharing of hundreds of millions of dollars worth of environmental monitoring data, much of it collected by environmental consultants on behalf of industry. By providing access to this usually **confidential data**, the **Industry Partners** are substantially enhancing WAMSI researchers' ability to determine the real-world impacts of dredging projects, and how they can best be managed. Rio Tinto's voluntary data contribution is particularly noteworthy, as it is not one of the funding contributors to the Node.

#### **Funding and critical data**



#### **Critical data**

**RioTinto**

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## **Front cover images (L-R)**

Image 1: Trailing Suction Hopper Dredge *Gateway* in operation during the Fremantle Port Inner Harbour and Channel Deepening Project. (Source: OEPA)

Image 2: Photograph of shallow water (<5 m) coral at Scott Reef, Western Australia. (Source: AIMS)

Image 3: Dredge Plume at Barrow Island. Image produced with data from the Japan Aerospace Exploration Agency (JAXA) Advanced Land Observing Satellite (ALOS) taken on 29 August 2010.

Image 4: Photograph of shallow water (<5 m) coral at Scott Reef, Western Australia. (Source: AIMS)

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## Executive Summary

Throughout the course of dredging programs, there are sometimes periods of increased environmental risk due to greater sensitivity of the local organisms to suspended and settling sediments. These more sensitive periods are often associated with reproduction and recruitment processes, and resource managers often try to protect these processes by temporarily restricting or stopping all turbidity-generating activities. The term ***critical window of environmental sensitivity (CWES)*** has been used in Western Australia to encompass this management approach<sup>1</sup>. The practice of managing dredging projects using discrete windows originated in the US in the early 1970s, where it is now used in approximately 80% of federal dredging projects<sup>2</sup>. The practice is contentious as it can significantly inflate costs for project sponsors and local stakeholders.

**One CWES is associated with the spawning of hard corals i.e. the phenomenon of synchronous, multi-specific mass release of gametes by broadcasting spawning species which occurs over a comparatively short period each year (the ‘window’).** When environmental regulations including a CWES for coral spawning were introduced in WA in the early 1990s (see text box below), little was known about the effects of sediments on the early life-history stages of corals – the approach was therefore precautionary. Since then, there have been a few studies on the effects of sediments on the early life-history stages but overall there has been a much greater understanding of the reproductive cycle and early life histories of corals.

**Text Box 1.** Location, start dates and volume (wet Mm<sup>3</sup>) of sediment removed in 19 major dredging projects in the Pilbara region of Western Australia, where there have been regulatory requirements with respect to the coral spawning *critical window of environmental sensitivity (CWES)* in either the WA Environmental Protection Authority Assessment Report or State Government Ministerial Statement (MS). All Ministerial Statements and Assessment Reports referred to below are searchable on the WA EPA website. The CEWS is defined as the number of days (d) following the commencement of spawning, or since 2007, includes days before spawning is predicted as well as days after it has started. Where: LPG and LNG refer to liquefied petroleum or liquefied natural gas. Expan. and Devel. refer to Port expansion and development.

Proposal	Development	Location	Date	Mm <sup>3</sup>	Rep.	MS	CWES
North West Shelf Project			Sep-79	3.2	694	na	Not specified
LPG Gas Extraction project	LNG Plant		Jul-93	0.70	724	320	
North West Shelf Gas Project			Dec-99	3.70	962	536	see notes
Dampier Port Authority		Mermaid Sound	Oct-03	4.61	1116	643	
Dampier Port Upgrade			Oct-03	3.10	1117	644	4 d
Pilbara Iron Ore	Port Expan.		May-05	4.67	1173	690	Not specified
Dampier Port Upgrade			Aug-06	3.45	1225	731	7 d
Cape Lambert Port Upgrade		Cape Lambert	Apr-07	3.60	1254	743	4 d
Pluto Development	LPG Plant	Mermaid Sound	Jul-07	14.0	1259	757	5 d (before) 3 d (after)
Anderson Point Port Upgrade	Port Expan.	Port Hedland	Apr-08	3.5	1286	771	
Finucane Island			Nov-08	3.9	1304	781	Not specified
Gorgon Gas Development	LNG plant	Barrow Island	Apr-09	7.6	1221	800	5 d before 7 d after
Nelson Point	Port Expan.	Port Hedland	Sep-09	6.7	1337	812	Not specified
Cape Lambert Port Upgrade B	Port Devel.	Cape Lambert	May-10	14.0	1357	840	3 d before 7 d after
Roy Hill 1 Iron Ore Project			Dec-10	0.0	1377	858	
South West Creek	Port Expan.	Port Hedland	Jan-11	14.2	1380	859	Not specified
Wheatstone Development	LNG plant		Jun-11	48.0	1404	873	3 d before 7 d after
Port Hedland Outer Harbour	Port Expan.	Onslow	Jan-12	42.03	1427	890	Not specified
Anketell Point	Port Devel.	Anketell Point	Jul-12	26.6	1445	930	3 d before 7 d after

<sup>1</sup> EPA (2016) Technical Guidance: Environmental Impact Assessment of Marine Dredging Proposals. Environmental Protection Authority, Perth, Western Australia. 76 pp

<sup>2</sup> Suedel BC, Kim J, Clarke DG, Linkov I (2008) A risk-informed decision framework for setting environmental windows for dredging projects. Sci Total Environ 403:1-11

To improve the ability to predict and manage the consequence of dredging during coral spawning periods, and provide guidance for a subsequent series of laboratory-based experiments (examining cause-effect and concentration-response relationships), **this study reviewed the effects of dredging activities on the reproduction of predominantly broadcast spawning corals.**

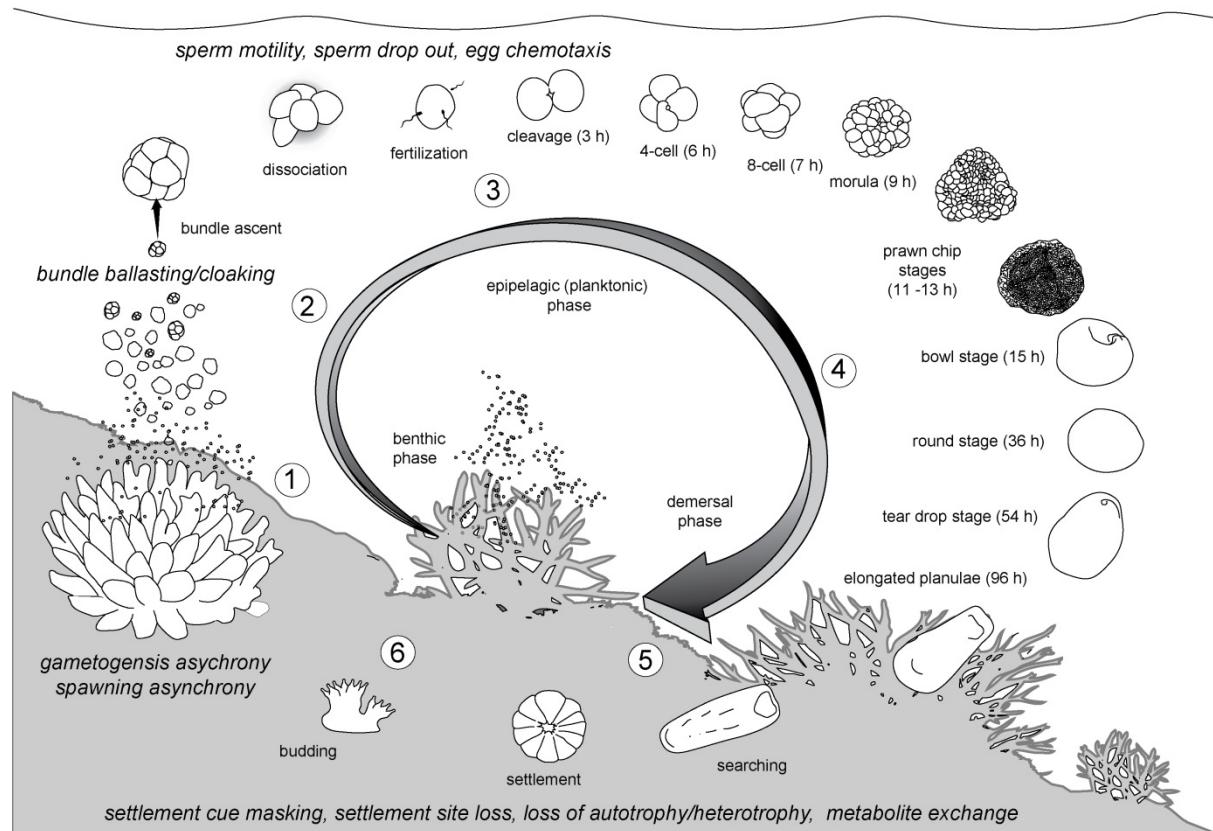


Figure 1. A stylised depiction of the reproductive cycle of a broadcast spawning Acropora species.

For the analysis, the life-cycle was divided into **six distinct stages** (shown schematically in Figure 1) including: (1) gametogenesis (spermatogenesis and oogenesis) and reproductive synchrony of the adults, (2) synchronisation of the spawning and release of egg-sperm bundles, (3) fertilisation of the eggs (4) embryogenesis and larval development, (5) settlement of the larvae and metamorphosis to the primary polyp, and (6) budding i.e. formation of daughter polyps and sexual maturation.

Each of these stages occur in different places, from the reef (**benthic phase**), the water surface, upper water column, the water column (collectively the **epipelagic or planktonic phase**), a short **demersal** phase where the mature larvae temporarily reside near the seabed searching for places to settle, and a final **benthic phase** as the now competent, mature larvae settle and undergo metamorphosis.

Each of the six stages also occur over different durations, and knowing the length of each is important for the design of environmentally realistic exposure experiments in future laboratory based studies (see below). For each stage, all available literature – 46 individual studies and involving 73 species of corals in total – was examined.

In general terms, the stages last a few **weeks/months** for gametogenesis of the adult colony; **minutes** for rising of the egg-sperm bundles to the surface and break-up of the bundle; **hours** until first cleavage (indicating fertilisation) and early stages of embryogenesis, **days** until movement occurs indicating ciliation (at which point the embryo is termed a larvae); **days/weeks** for the larvae to reach competency and settle on the reef; **weeks/months** for budding (asexual reproduction) of the primary polyp to occur; and **years** for corals to become sexually mature.

We then considered how dredging activities could affect each of the six stages, identifying known mechanisms — **cause–effect pathways** — and also putative or **biologically plausible mechanisms**. These are as yet untested mechanisms, but where there is a **credible or reasonable biological and/or toxicological basis linking the proposed cause and effect**. Both positive and negative mechanisms were included.

As a framework for this complex interaction (of each life-history stage and each different potential stressor) we applied the **US EPAs causal/diagnosis decision information system (CADDIS<sup>3</sup>)**. The system allows identification of what are the key proximal stressors, steps in a causal pathway, modes of action and effects, and when displayed graphically (Figure 2), produces a conceptual model indicating how they are interlinked, and the relationship with other interacting factors.

### Causal/diagnosis decision information system (CADDIS) framework

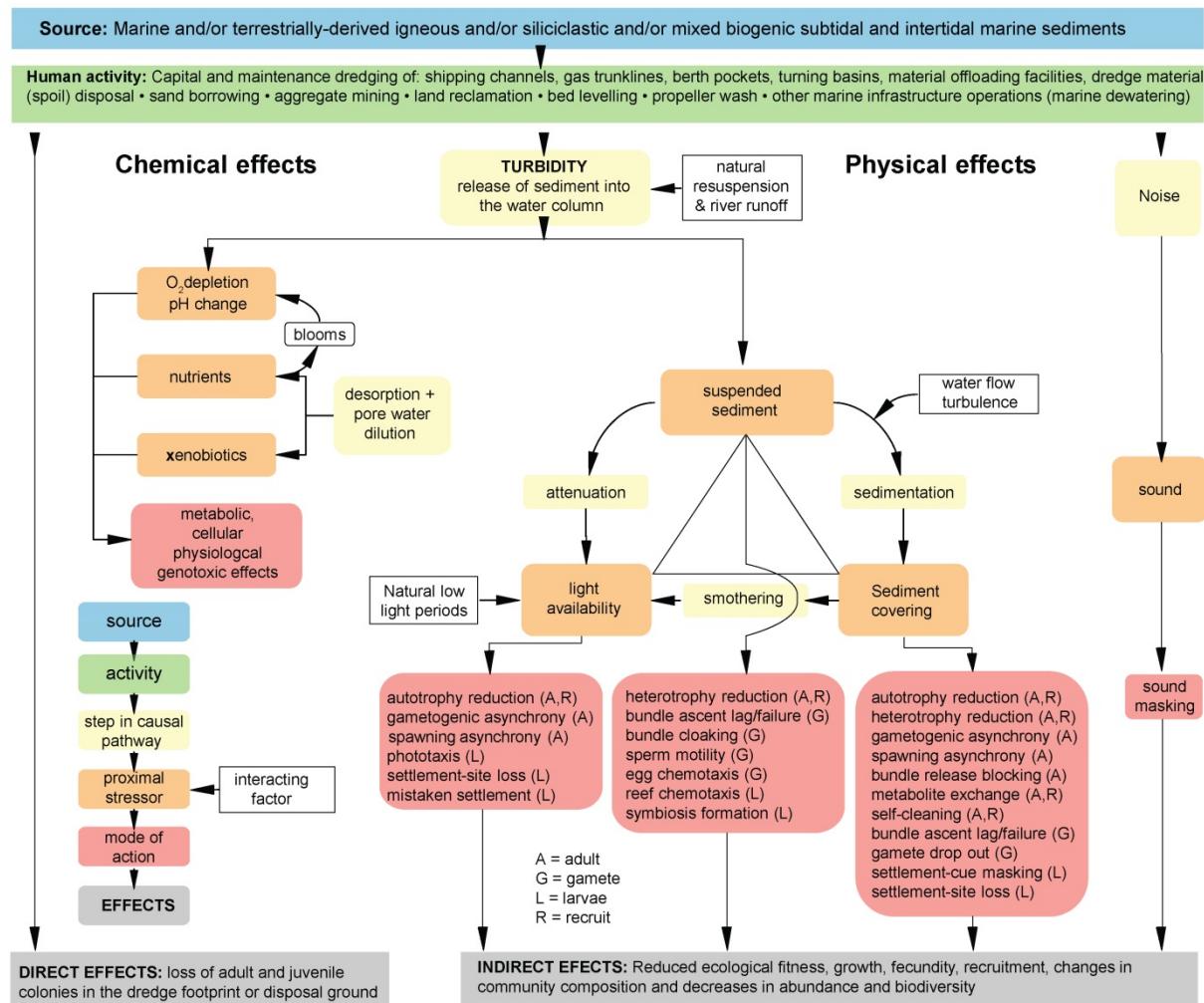


Figure 2. Conceptual model of the effects of dredging activity on the early life-history stages of corals, as well as proximal stressors, interacting stressors are depicted along with modes of action and likely physiological and ecological responses (see text for explanation). G = gametes, L = larvae, R = recruits and A = adults.

From the model one group of mechanisms was referred to as **chemical effects**, and involved chronic toxicological, cellular and physiological effects associated with chemical contamination of the sediments and also the release of nutrients and depletion of oxygen. These were considered important; however, as many capital dredging projects in the WA tropics are green-field sites (without historical contamination) they were considered of

<sup>3</sup> Norton SB, Cormier SM, Suter GW, Schofield K, Yuan L, Shaw-Allen P, Ziegler CR (2009). CADDIS: the causal analysis/diagnosis decision information system. Decision support systems for risk-based management of contaminated sites. Springer, pp. 1–24.

secondary importance compared to the majority of mechanisms which were referred to as **physical effects**. One of the physical effects involved the effects of noise from the propellers, pumps and engines of dredges masking the sound of fish calls, grunts and snapping of shrimps. There is evidence that some pelagic coral larvae use sound to locate a reef for settlement. This cause–effect pathway was referred to as *sound masking*, and while it is interesting as it is the only pathway not involving turbidity generation, it was also considered to be of secondary importance compared to the many physical effects associated with the generation of sediment plumes.

For the physical effects, the primary **stressors** were **elevated suspended sediment concentrations (SSCs)**, **light reduction** and **elevated levels of sediment deposition**. Some potential positive effects were identified, such as a reduction in UV light penetration from high water turbidity which could reduce DNA damage to gametes and embryos near the surface. However, **the overwhelming majority of the known or plausible effects on the adults, gametes, embryos, larvae and new recruits (30+)** were negative.

Mechanisms associated with turbidity include the effects of light reduction on both the allocation of energy to gametogenesis and the synchronisation of oogenesis or spermatogenesis (collectively called *gametogenic asynchrony*). The coordinated release of gametes (spawning) is also thought to be influenced by light, and water column turbidity could affect the harmonization and synchronization processes culminating in the highly coordinated near-simultaneous release of gametes by a population (*spawning asynchrony*).

The physical effects also included **a suite of previously unrecognized cause-effect pathways involving an interaction of suspended sediments with the egg-sperm bundles, eggs and sperm**. It was considered plausible that sediments could stick to the egg-sperm bundles, delaying or preventing their ascent to the surface (i.e. *bundle ascent lag* and *ascent failure* – collectively referred to as *bundle ballasting*), and also prevent or delay the break-up of the bundle (*bundle cloaking*). Sediment could also act as a physical barrier between the sperm and the eggs (*sperm motility*) and by binding to the eggs, mask activation and attraction cues (*egg chemotaxis*). Sperm could also become entangled in sediment which could settle out of suspension, separating the already negatively buoyant sperm from the positively buoyant eggs (*sperm-drop out*). Collectively all these mechanisms could reduce the chances of egg-sperm interaction, reducing the chances of fertilization success and the total number of individuals moving on to further demographic stages.

**Fewer cause–effect pathways were identified in the post-fertilization embryogenesis and larval development stages**, when the larvae were in the water column, although high SSCs could affect feeding of the developing larvae and cause larvae to expend important energy resources on avoiding suspended sediments or produce mucus to remove sticky sediments.

**Another larger suite of mechanisms were recognized at the settlement phase**. Sediment could mask or cover larval settlement cues such as crustose coralline algae (*settlement cue masking*). Elevated turbidity could reduce the photic zone, thereby reducing the area available for larvae to settle (*settlement site loss*), or cause the larvae to settle in areas where the average light conditions do not favour their long-term survival once the water clarity returns to normal (*mistaken settlement*). This also encompasses a negative tactile response to unconsolidated sediment and larvae settling in and on sediment-free refuges (cracks and crevices and underhangs) which may be suboptimal for subsequent long-term survival of the juveniles. **The cause–effect pathways associated with effects of sediment smothering of the new recruits were considered likely to be similar to those of the adult corals**, including reduced autotrophic and heterotrophic feeding (*loss of autotrophy/heterotrophy*), and reduced gas/metabolite exchange (*metabolite exchange*).

Finally, for each of the size stages of the reproductive cycle, the **published literature was then reviewed with particular consideration of the experimental methodology, sediment types, exposure concentrations and duration, limitations of the study and ability to generate concentration-response relationships to improve impact prediction**. In total, only **12** individual published scientific reports (5 field-based and 7 laboratory-based studies) were found which could provide some relevant information on the 6 stages of the life cycle. These include effects on gametogenesis and reproductive synchrony (**3 studies**), fertilization (**3 studies**), embryogenesis and larval development (**2 studies**), settlement and metamorphosis (**6 studies**), and survival of the new recruits

(1 study). The studies involved **7 different coral species** with the broadcast spawning species *Acropora millepora* (4 studies) and the brooding species *Pocillopora damicornis* (3 studies) the most commonly used. Since 2000 there have only been 4 published reports on this topic.

The field studies were mostly correlative (i.e. reduced fecundity in naturally turbid areas) and for the more manipulative, laboratory based studies it was **difficult to establish concentration-response relationships as the sediment concentrations and sediment particle sizes (and chemical content) were not always reported**. None of the studies considered **concentration–response relationships but used statistical testing of a few different sediment concentrations**.

For the effects of sediments on **fertilisation** there was **considerable variability** between studies, which may be related to the sediment type. **However, the variability could also be due to the different methodological approaches, such as egg and sperm concentrations and egg-sperm contact time, which are known to affect the experimental outcome.** These issues need to be considered in the interpretation of the results of future studies. Approximately half of the studies examined the effects of sediments on settlement, showing that **coral larvae prefer not to settle where there is loose, unconsolidated sediment**. However, the studies did not determine the proximate stressor that affects settlement preference (e.g. did the mechanism involve suspended particles or sediments accumulating on the substrate), and in most cases, only one proximate stressor was measured (i.e. suspended sediments or sediment deposition rate).

As a broad generalization, **embryogenesis and larval development stages appear to be less sensitive to elevated suspended sediment concentrations than the fertilisation stage**, but more studies are needed to verify this. Settlement appears to be a very sensitive stage. **There is also critical lack of information on the effects of dredging activities on early post-settlement survival in the weeks to months after settling.**

## Considerations for predicting and managing the impacts of dredging

**The causal/diagnosis decision information system (CADDIS) framework used in the review proved useful for identifying areas of uncertainty, knowledge gaps and for guiding future laboratory or field studies.** Approximately 30+ mechanisms were identified, including many suggested or putative (biologically plausible) mechanisms which have not yet been tested. Each mechanism operates over different time periods ranging from hours to several weeks. Recent analyses of water quality during several major dredging programs<sup>4,5</sup>, have provided relevant information on the mean, median and 80<sup>th</sup>, 95<sup>th</sup> and 100<sup>th</sup> percentiles of SSCs and benthic light availability over the same running mean time period (hours to weeks). **This information can be used to design environmentally relevant exposure experiments (see <sup>6</sup>) to test these mechanisms and to derive concentration – response relationships<sup>7</sup>.**

The CADDIS framework also highlighted some of the difficulties associated with establishing concentration–response relationships for sediments and in particular, **the conflation of proximal stressors which could potentially confound establishing causal links**. This needs to be **carefully considered when interpreting the results of past laboratory or field manipulations** for risk assessment purposes. Thus, while some of the stressors are distinct, such as effects of noise, other proximal stressors are highly interlinked. For example, a high suspended sediment concentration could be a stressor by itself, but high sediment concentrations would strongly attenuate light (a step in the causal pathway) resulting in light limitation, which is another stressor for corals. In such a case it would be difficult to determine what is causing the observed biological effects, the elevated SSCs

<sup>4</sup> Jones R, Fisher R, Stark C, Ridd P (2015) Temporal patterns in seawater quality from dredging in tropical environments. PloS one 10.10 (2015): e0137112.

<sup>5</sup> Fisher R, Stark C, Ridd P, Jones R (2015) Spatial patterns in water quality changes during dredging in tropical environments. PloS one 10.12 (2015): e0143309.

<sup>6</sup> Harris CA, Scott AP, Johnson AC, Panter GH, Sheahan D, Roberts M, Sumpter JP (2014) Principles of sound ecotoxicology. Environ. Sci. Technol. 48, 3100–3111.

<sup>7</sup> Using this approach, some of these mechanisms – bundle ballasting, sperm drop-out, sperm motility, settlement cue masking – have been tested in the laboratory based experiments examining effects of sediments on fertilization, embryogenesis/larval development, settlement.

or the associated light reduction or both. **The pooling of results from past studies, as is common in review articles, can be very misleading unless the wider context of the treatment on other causal pathways is known: only then can the results be used with confidence in an environmental context.**

Because of this problem of conflation, future studies should pay specific attention to the cause–effect pathways i.e. **the mechanism associated with any effects**. Where appropriate, **statistical metrics such as EC<sub>10</sub> and EC<sub>50</sub> values should be derived rather than statistical testing of a few point concentrations**. It is essential that **SSCs are quantified gravimetrically (as opposed to being expressed nominally)**. The vast majority of sediments that disperse away from the operating dredge or disposal grounds are fine in grain size (<63 µm), and future studies should use **suitably sized sediment particles**, and undertake **analyses of particle size distributions**. Future studies should also undertake a full suite of **organic and inorganic chemical analyses** as part of normal ecotoxicological procedures to discount the potential effects of any legacy contaminants. Chemical analyses should be conducted of the typically fine clay and silt fractions used in the assays and not the coarser, bulk surficial sediments from the collection point. The use of clean aragonite or calcium carbonate sediments are recommended as positive controls and surrogates for sediments (such as carborundum, kaolin and bentonite clay) should not be used for establishing dose-response relationships.

### **The coral spawning critical window of environmental sensitivity (CWES)**

The coral spawning critical window of environmental sensitivity (CWES) was introduced in 1993, nearly 25 years ago. As indicated in the text box below, **it has evolved historically, presumably as new information became available and has tended to become more prescriptive over time (but see further below)**. Significant changes include being more precise over stoppage time (from 2003 onwards), recognizing biannual as opposed to annual spawning (from 2006 onwards), requiring proponents to stop dredging activities before the predicted night of spawning to allow suspended sediments to settle out of suspension (from 2007 onwards), and approximately **doubling of the length of the window from 4 d (after the first night of spawning) to 7 d (from 2009 onwards)**.

The window as it currently stands (3 d before until 7 d after the predicted night of coral spawning) covers the majority of time when the gametes, embryos and larvae are in the water column. However, based on the analysis of settlement patterns from ~20+ studies in this report, **it is probably too short to fully accommodate the settlement stage, especially if corals spawn over several nights**. Extending the window seems an obvious solution to fully cover the larval settlement period, but the next question becomes when to close the window.

Naturally high levels of post-settlement mortality is a well-known characteristic of most free-spawning marine invertebrates<sup>8</sup>. Corals are also known to have high levels of natural early post-settlement mortality but it is nevertheless one of the most poorly understood stages of the reproductive cycle. For corals, **the first few weeks and months after settling are critical** as the sub-millimetre sized coral polyps typically acquire their dinoflagellate microalgal symbionts forming the symbiosis (holobiont). They start gaining energy phototrophically, as well as heterotrophically through particle-feeding and zooplanktivory, and through enhanced calcification associated with the symbiosis, develop secondary polyps and complex three-dimensional skeletons. During the early stages of this period **they are vulnerable to the same stressors as the adult corals, but it is expected that they would be much more sensitive to turbidity (especially to sediment deposition) because of their diminutive size and limited energy reserves**.

**The success of a coral spawning CWES as a management tool should ultimately be assessed in terms of the recruitment success of juveniles into the next generation.** There is no compelling reason for solely protecting the planktonic stages (when the gametes and embryos/larvae are in the water column), as opposed to all potential demographic bottlenecks associated with recruitment, especially settlement and early post-settlement survival. An obvious step would be to **extend the coral spawning CWES for a few months to fully cover the settlement period and the initial settlement stages as the corals begin to bud and gain size**.

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<sup>8</sup> Gosselin LA, Pei-Yuan Q. (1997) Juvenile mortality in benthic marine invertebrates. Marine Ecology Progress Series 146: 265-282

### Text Box 2. History of the Coral Spawning CWES

The first regulatory requirements for dredging proponents to consider coral spawning was in **1993**, following an application to dredge Mermaid Sound (Dampier Archipelago) to provide ship access to a new LPG Gas extraction and export plant (see EPA Bulletins 694 and 724). The associated Ministerial Statement (that a proposal may be implemented pursuant to the provisions of the Environmental Protection Act (1986)), stipulated that '*...dredging should be undertaken at an appropriate time and in such a manner that there is no significant impact on coral spawning in the area, to the requirement of the Minister for the Environment on advice of the Environment Protection Authority...*' (Table 1, MS 320). A subsequent application for an LNG plant on the Burrup Peninsula in **1999** contained a similar clause including '*...not dredging for a suitable time period around the actual coral spawning event...*' with the stoppage time to be managed in consultation with the state government environmental offices (Table 1, MS 536).

In **2003**, the Ministerial Statements from two overlapping dredging programs in the Dampier Archipelago were more prescriptive over stoppage times, with both containing conditions to cease dredging and/or spoil dredging activities for a 4 day period associated with the spring coral spawning period. The four day period was specified (as exact dates) in the statements, but the ultimate timing of the window could be varied upon consultation with the EPA and on the basis of the investigations into the timing and extent of coral mass spawning (see Table Ministerial Statements 643 and 644).

The next significant development was the recognition that there are two main spawning events in WA, a primary one in autumn and a secondary, minor one in spring (see also <sup>9</sup>). The Dampier Port Upgrade proposal in **2006** included a ministerial condition stipulating that the dredging should cease during the autumn spawning but could occur during the spring period, but only if the proponent could demonstrate the corals within the area of influence of the dredge or spoil plumes are not significantly participating in a spring coral spawning (MS 731).

In the conditions for the next dredging project (**2007**, Cape Lambert Project) no distinction was made between the major and minor spawning periods with dredging required to cease if corals within the area of influence of the dredge or spoil plumes were significantly participating in a coral spawning event (MS 743). In these projects, the duration of any stoppages were not specified in the Ministerial Statements but the accompanying EPA report and recommendations identified several 7 day periods that spawning could occur after the full moon in spring. The proponents were required to identify the periods within a project-specific coral spawning management plan prepared for, and presumably endorsed by, the then local state environment body (Bulletin 1225).

In July **2007**, stoppage times for Woodside's Pluto LNG proposal were again explicitly stated in the Ministerial Statement. There was a requirement for a management framework that identified autumn and other potential mass spawning periods, and the regulations required that all turbidity-generating events were to cease from 5 days before the predicted coral spawning events to 3 days after completion of the spawning events to allow for '*...fertilisation, larval competency and settlement (MS 757)...*'. This requirement to cease activities before spawning was a recognition of time needed for any sediment plumes to dissipate to acceptable water quality levels.

The Gorgon (Barrow Island) (MS 800, **2009**) and Cape Lambert Port upgrade (MS 840, **2010**) projects had conditions requiring a '*...cessation...*' of all turbidity-generation events during the autumn and spring spawning periods for 5 days before and 7 days after spawning period in the case of the Gorgon project, and for 3 days before and 7 days afterwards for the Cape Lambert B project.

Finally, the Ministerial Statements for the Wheatstone LNG processing plant and Anketell Point Iron port development contain near identical conditions for ceasing of dredging and dredge spoil disposal (i.e. turbidity-generating activities) for 3 days prior to the predicted commencement of mass coral spawning, for until 7 days from the commencement of mass coral spawning. However, both ministerial statements contain a clause permitting turbidity-generating activities if proponents supply '*...peer-reviewed scientific evidence that if those turbidity generated activities were to continue during coral mass spawning events, any effect, if it were to occur, would not significantly impact the functional ecology of local and regional reefs...*'.

<sup>9</sup> Gilmour J, Speed CW and Babcock R (2016) Coral reproduction in Western Australia. PeerJ 4:e2010; DOI 10.7717/peerj.2010.

Such an extended window should be relatively easy to accommodate during maintenance dredging, and setting the starting dates of capital dredging projects as to not coincide with coral spawning and settlement periods would constitute a best management practice. However, for extended capital dredging projects that last >1 year, **extending the coral spawning CWES would significantly limit the time that turbidity-generating activities could occur near coral reefs in any given year, increasing the overall length of the program and with that the total duration of disturbance.** The question is then whether the extended window is **reasonably practicable**, and whether the resulting intermittent and protracted dredging operation would result in a better net environmental benefit than a well-managed shorter campaign

One of the most contentious issues of the coral spawning CWES for long-term capital dredging projects has been that **all turbidity generating activities must temporarily cease**, which has tangible cost implications for proponents. The most recently issued approval conditions (Ministerial Statements 873 and 930) still contain a very prescriptive clause regarding stopping dredging during coral spawning periods i.e. '*...shall not conduct turbidity-generating activities...*' for 3 d before and 7 d after the predicted night of spawning (see above). However, the conditions also include a much more objective clause that turbidity-generating activities are allowed to occur if proponents supply '*..evidence that if those turbidity generating activities were to continue during coral mass spawning events, any effect, if it were to occur, would not significantly impact the functional ecology of local and regional reefs...*'. This latter approach is taking a much more holistic view of coral spawning CWES **recognizing the importance of recruitment to the next generation** discussed previously, as opposed to simply the protection of the short time period when the gametes and embryos/larvae are in the water column.

The clause is significant as it opens up the possibility for dredging during spawning periods and dredging proponents are effectively being offered the opportunity to manage coral spawning periods in much the same way as for adult corals: by understanding water quality (the intensity, duration and frequency of pressure fields), the location of sensitive receptors (in space and time), and through an understanding of cause-effect pathways and concentration-response relationships, using thresholds to estimate the consequence of their activities. Dredge management options to reduce the pressure include separating the dredging and disposal activities from areas where plumes may encounter coral spawn slicks, and if needed, minimizing turbidity generation such as reducing or shortening overflow periods, reducing production rates and/or using different types of dredges.

## Residual Knowledge Gaps

Nevertheless what is still lacking is detailed empirical information on the effects of sediments on the various life-history stages over **appropriate time frames**, to be able to methodically assess the possible consequences of different dredging scenarios (dredging locations, equipment type, disposal options) on the various life-history stages to sediment. Addressing this knowledge gap has already been started in the subsequent laboratory based experiments examining effects of sediments on fertilisation, embryogenesis and larval development, and settlement.



## Review

## Effects of sediments on the reproductive cycle of corals

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## ABSTRACT

Dredging, river plumes and natural resuspension events can release sediments into the water column where they exert a range of effects on underlying communities. In this review we examine possible cause–effect pathways whereby light reduction, elevated suspended sediments and sediment deposition could affect the reproductive cycle and early life histories of corals. The majority of reported or likely effects (30+) were negative, including a suite of previously unrecognized effects on gametes. The length of each phase of the life-cycle was also examined together with analysis of water quality conditions that can occur during a dredging project over equivalent durations, providing a range of environmentally relevant exposure scenarios for future testing. The review emphasizes the need to: (a) accurately quantify exposure conditions, (b) identify the mechanism of any effects in future studies, and (c) recognize the close interlinking of proximate factors which could confound interpretation of studies.

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## 1. Introduction

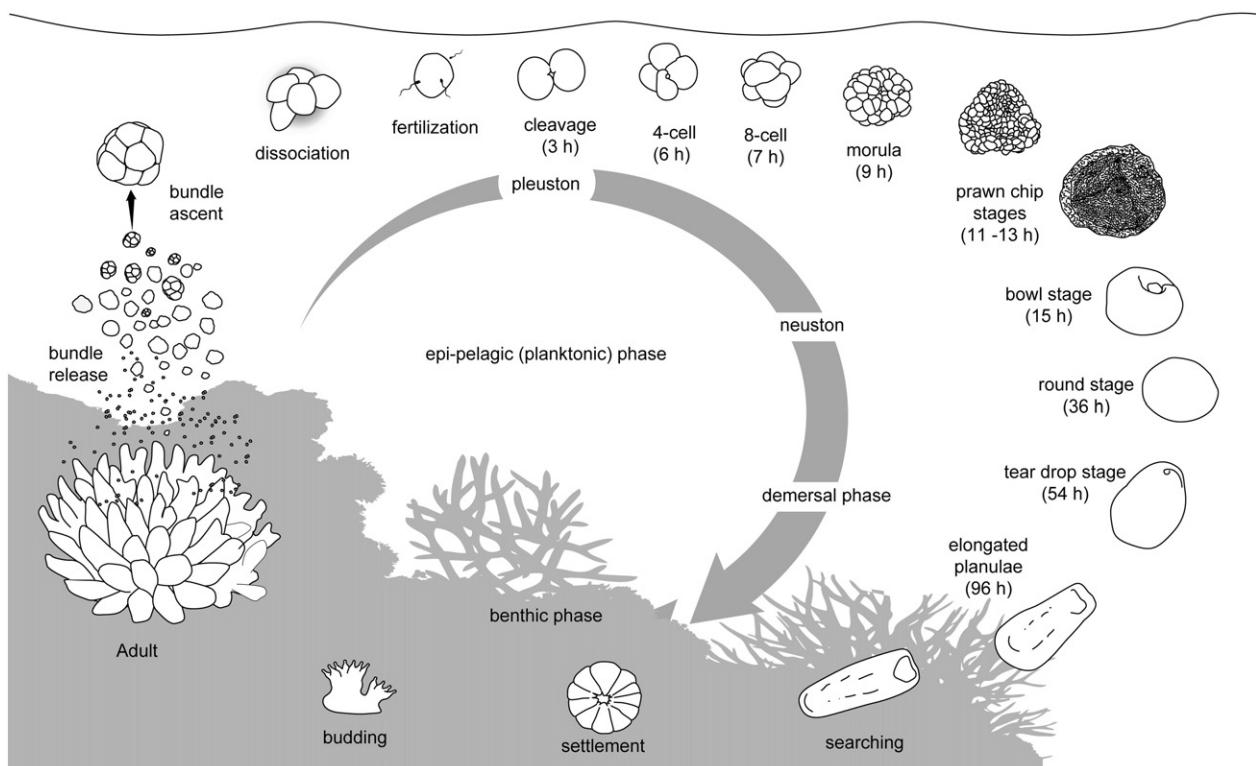
Natural resuspension events, terrestrial run-off and dredging-related activities can temporarily increase suspended sediment concentrations (SSCs) in the water column. The effects of suspended sediments on adult corals are well known (Erftemeijer et al., 2012a; Rogers, 1990) but nevertheless constitute only part of the demographic equation (Hughes et al., 2000, 2011). The sensitivity of the early life-history stages of corals has also been recognized for over a century (Stephenson, 1931; Wood-Jones, 1910), but even before fertilization, embryogenesis and the establishment of the sessile, and benthic juvenile form, sediments could exert a range of effects on the reproductive cycle including gametogenesis, spawning synchrony and on gametes in the water column.

This review examines the effects of turbidity on all aspects of the coral life cycle of corals from gamete development to the early post-settlement stage. The focus is on the effects of sediments on broadcast spawning species which usually dominate the tropical coral reef environment. Their life cycle is complex involving gametogenesis, reproductive synchronization, fertilization at the surface and larval development in the water column, leading finally to settlement and metamorphosis into a sessile polyp. Their life-cycle is stylized in Fig. 1 and based on *Acropora* spp.

Natural resuspension events regularly occur in the shallow, tropical marine environment (Anthony et al., 2004) and although resuspension and transport of suspended material may be strongly influenced by unidirectional currents, wind-driven waves are the primary mechanism of turbidity generation in the shallow reef environment (Jing and Ridd, 1996; Larcombe et al., 1995, 2001; Lawrence et al., 2004; Ongston et al.,

2004; Verspecht and Pattiarchi, 2010). In the shallow inshore turbid zone of the Great Barrier Reef, resuspension of bottom sediment by waves affects coral communities on an estimated 110 days year<sup>-1</sup> (Orpin et al., 1999). During predicted coral spawning periods wind speeds have averaged 8–10 m s<sup>-1</sup> (or 15–20 knots) on six out of eleven years from 2000–2010 (AIMS, 2011). At these wind speeds natural resuspension and wind-wave induced turbidity would occur in the inshore turbid zones (Larcombe et al., 1995; Orpin et al., 2004; Orpin and Ridd, 2012) with possible implications for spawning and recruitment success of local corals.

In addition to natural events, anthropogenic activities can also release sediment into the water column, and dredging and disposal of dredged material (spoil) are the most well-known sources and are also the most amenable to management. In recognition of the sensitivity of the early life-cycle stages of corals, and since reproduction and recruitment processes underpin the maintenance and resilience of communities to disturbance, policy makers have attempted to protect coral spawning periods from sediments generated by dredging-related activities. Since 1993 dredging projects in Western Australia that are close to reefs are required to temporarily stop when corals are spawning (Baird et al., 2011; EPA, 2011). This regulatory condition is currently set as 5 days before spawning to 7 days afterwards. This is referred to as the coral spawning environmental window (EW) and is associated with the well-known synchronous, multi-specific release of gametes by broadcasting spawning coral species that can occur in WA in single epidemic events of relatively short duration (EPA, 2011; Simpson, 1985; Styan and Rosser, 2012). Unfavorable conditions during a spawning period could result in loss of the entire reproductive output for the year (Harrison et al., 1984). This management approach has also been adopted



**Fig. 1.** A stylized depiction of the reproductive cycle of the broadcast spawning *Acropora* species with indicative timings based on the studies of Hayashibara et al. (1997), Okubo and Motokawa (2007), Okubo et al. (2008) and Ball et al. (2002). The cycle begins and ends with gametogenesis in the adult colonies on the reef, but in between there are a complex sequence of phases which are spatially and temporally separated. Spawning occurs through the release of positively buoyant membrane-less, mucous bound egg and sperm bundles which dissociate at the surface and upper water column releasing the eggs and sperm. Fertilization occurs at the surface and upper water column where the initial stages of embryogenesis occur. Cleavage takes place by progressive furrow formation and the embryos of most *Acropora* species undergo an relatively unorderd, irregular division cycle after the 8-cell stage eventually and after the morula stage becomes a convex-concave cellular bi-layer stage (the prawn-chip stage sensu Hayashibara et al., 1997) then bowl stage. The embryos then fatten to become a roughly spherical shape and by 36 h develop cilia over the epidermis, which beat synchronously imparting mobility to the planulae larvae. The larvae then become progressively elongated and begin searching substrata and eventually settle and undergo metamorphosis into juvenile polyps.

in some dredging projects on the Great Barrier Reef (Koskela et al., 2002) and the possibility of introducing this practice to other locations such as Singapore has been suggested (Erfemeijer et al., 2012b).

This management approach is highly contentious internationally as it can significantly inflate costs for project sponsors (Suedel et al., 2008). One of the most contested issues is the length of the window and also whether dredging-related turbidity-generating activities need to cease entirely or whether dredging can continue but must adhere to more conservative water quality guidelines. Addressing these issues associated with a coral spawning environmental window is technically challenging as it requires an understanding of how all possible proximate stressors (causal agents) associated with turbidity generation can directly or indirectly influence all stages in the coral reproductive cycle. Over the last 20 years there have been several studies examining the effects of sediments on the early life-cycle stages, but perhaps more importantly there is now a much greater understanding of the reproductive biology of corals. It is now possible to more fully examine the mechanisms where sediments could affect the reproductive cycle (i.e. cause–effect pathways) and also to identify biologically plausible mechanisms. In epidemiology, biologically plausible mechanisms are those where there is a credible or reasonable biological and/or toxicological basis linking the proposed cause and effect (Adams, 2005; Hill, 1965; Suter, 2006).

This review focuses on the biology of the reproductive cycle that could be susceptible to effects of sediments (including high SSCs, sediment deposition, and changes in light quality and quantity) and other dredging-associated pressures (including sound and sediment contamination). For orientation purposes within this review, we first describe each stage of the life-cycle from gametogenesis to post-settlement survival, describe past studies, and then use this information to generate the conceptual model of known and plausible cause–effect pathways. Testing the cause–effect pathways requires a knowledge of where the processes occur (benthos, water surface, water column), and the length of each of the stages, so information is included on the duration of these phases where available. For experimental testing of each of the stages it is also necessary to know what the environmentally realistic or relevant exposure conditions (SSCs, light reduction, etc.) are over the relevant time frames for each stage. There is surprisingly little published information on water quality conditions that can occur during dredging programs on a coral reef to frame such an analysis. For contextual purposes, the review therefore starts with a brief description of water quality conditions from a recent large scale dredging project in the Pilbara region of Western Australia.

## 2. Example of water quality conditions during a large dredging program

The Barrow Island dredging project in NW Australia is one of the largest and well-studied dredging projects undertaken in a clear-water, coral reef environment, and involved the removal of ~8 Mm<sup>3</sup> of sediment to create an access channel for a liquefied natural gas (LNG) gas plant (Evans et al., 2012; Hanley, 2011). Spatial and temporal scales of SSC dynamics in dredging programs are highly dependent on distance from the dredge, the dredging method, mode of operation(s), type of sediment dredged and the local hydro-meteorological (metocean) conditions (Black and Parry, 1999; Collins, 1995; Havis, 1988; Herbich and Brahme, 1991; Spearman et al., 2007). Data from the Barrow Island project (Fig. 2) show that natural background SSC levels are typically low <5 mg L<sup>-1</sup>, with episodic increase associated with storms and wind-wave re-suspension events (Fig. 2A). During dredging, and a few hundred meters away from a working trailing suction hopper dredge (TSHD), SSC levels can increase by 1–2 orders of magnitude with instantaneous values regularly exceeding 100 mg L<sup>-1</sup> and maximum instantaneous readings exceeding 200 mg L<sup>-1</sup>. As the time averaging period increases to 30 d, the maximum average SSCs decrease to <20 mg L<sup>-1</sup> (Fig. 2A).

Daily Light Integrals (DLIs) during the baseline period ranged seasonally from typically 1–10 mol m<sup>-2</sup> with occasional very low light periods occurring during the austral winter time (Fig. 2B). During the dredging period DLIs regularly fell below 1 mol quanta m<sup>-2</sup> and corals were occasionally exposed to extended periods of semi-dark, caliginous, twilight periods. In one of the worst periods the irradiance levels did not exceed 0.3 mol m<sup>-2</sup> over a 21 day period which is equivalent to an average daytime instantaneous flux of <10 µmol quanta m<sup>-2</sup> s<sup>-1</sup> (Fig. 2B).

## 3. Gametogenesis and reproductive synchrony

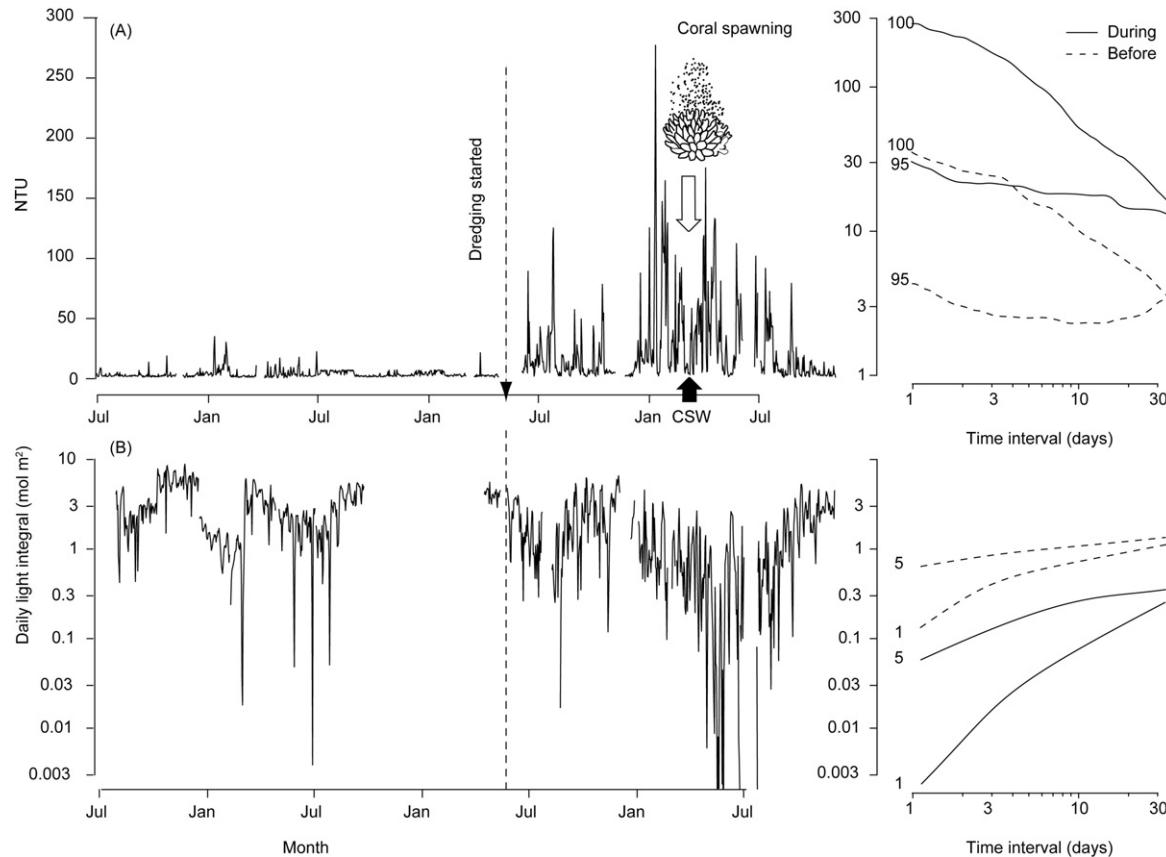
Scleractinian corals vary in their breeding systems, having either separate sexes (gonochorism) or combined sexes i.e. simultaneous hermaphroditism. Corals also vary in their mode of development and are either broadcast spawning species (spawners) which release gametes for external fertilization and with subsequent embryo and larval development in the planktonic phase, or breeding/brooding species, which have internal fertilization, brood embryos and develop planula larvae within their polyps (Fadlallah, 1983; Harrison and Wallace, 1990; Richmond and Hunter, 1990). These combinations (gonochorism versus hermaphroditism and spawners versus brooders) result in four basic patterns of sexual reproduction, and of the nearly four hundred species of corals examined to date approximately ~63% are hermaphroditic spawners (Baird et al., 2009; Harrison, 2011; Harrison and Wallace, 1990; Richmond and Hunter, 1990).

The timing of gametogenesis leading up to reproductive synchrony is depicted on the left of Fig. 3 with gonad production in the benthic, polyp phase typically occurring over a period of <12 months culminating in the annual coral spawning event. In most hermaphroditic species, oogenesis occurs over a period of months while spermatogenesis occurs more rapidly just prior to spawning and can be completed in a few weeks (Harriott, 1983; Harrison et al., 1984; Harrison and Wallace, 1990; Kojis and Quinn, 1982; Richmond and Hunter, 1990; Wallace, 1985b). Many broadcast spawning species synchronize their gametogenic cycles to potentially reduce predation (predator satiation) by planktivorous fish or filter feeders including other corals (Babcock et al., 1986; Baird et al., 2009; Harrison, 2011; Harrison et al., 1984; Harrison and Wallace, 1990; Hughes et al., 2000; Oliver et al., 1988; Pratchett et al., 2001). Spawning can also be synchronous between many different species and families of corals. This is the basis of the well-known multispecific, synchronous, coral spawning events, first identified in the early 1980s on the Great Barrier Reef (GBR) and involving at least 133 species of coral from ten scleractinian families (Harrison et al., 1984; Babcock et al., 1986; Willis et al., 1985; Harrison and Wallace, 1990). Change in sea surface temperature (Hayashibara et al., 1993), and solar insolation (Penland et al., 2004; Van Woesik et al., 2006), may constitute the proximate environmental cue(s) that instigates oogenesis, and temperatures over subsequent months may also affect the duration of oocyte development (Nozawa, 2012). Since its discovery, multispecific spawning events have increasingly been recorded in the Indo-Pacific and many other regions i.e. Caribbean, Japan, Gulf of Mexico (Baird and Guest, 2009; Baird et al., 2009; Harrison, 2011; Hayashibara et al., 1993).

### 3.1. Effects of sediment on gametogenesis and reproductive synchrony

No studies have directly manipulated SSC and sedimentation levels to examine the effects on gametogenesis, however several studies have correlated reproductive output with turbidity or sedimentation (Kojis and Quinn, 1984; Tomascik and Sander, 1987). Inferences were based on correlation (which does not prove causality) and using a similar approach Padilla-Gamiño et al. (2014) did not find any differences in gamete production in *Montipora capitata* in Hawaii in areas with different sediment trap accumulation rates.

The proposed mechanisms for decreased reproductive output were: (i) increased energy expenditure for self-cleaning, and (ii) that a



**Fig. 2.** (A) Nephelometric turbidity units (NTUs) collected every 10 min and (B) Daily Light Integral (DLI, mol m<sup>-2</sup>) calculated from instantaneous fluxes collected from sensor platforms mounted 0.4 m above the seabed at 6–9 m depth at 3 locations <500 m away for a dredge during the Barrow Island (Pilbara, Western Australia) dredging project in the baseline (pre-dredging period) or during the 1.5 year dredging program. Figures on the right hand side show the 95th and 100th (maximum) percentiles of the NTUs for different running mean periods (from 1 h–30 days) before (dashed lines) and during (solid lines) the dredging program or the 5th and 1st percentiles of DLI (mol photon m<sup>-2</sup>). Nephelometer turbidity units (NTUs) can be converted to SSCs using a conversion factor of 1.3 to 1.6 determined from regressions of SSC (assessed gravimetrically) versus NTU (nephelometer) readings. The Barrow Island project involved the excavation of ~7.6 Mm<sup>3</sup> of sediment dredged over 530 days from 19 May 2010 to 31 October 2011. The dredging occurred on a 7 days × 24 h basis, using a combination of trailer suction and cutter suction dredges and back hoes. Dredging stopped only for maintenance and bunkering requirements, the passage of cyclones and storms and over the coral spawning window (CSW) which was from 20–31 March 2011 (see arrows in Fig. 2A). The Ministerial approval statement for this dredging project (MS800) is searchable on the WA EPA website (<http://www.epa.wa.gov.au>).

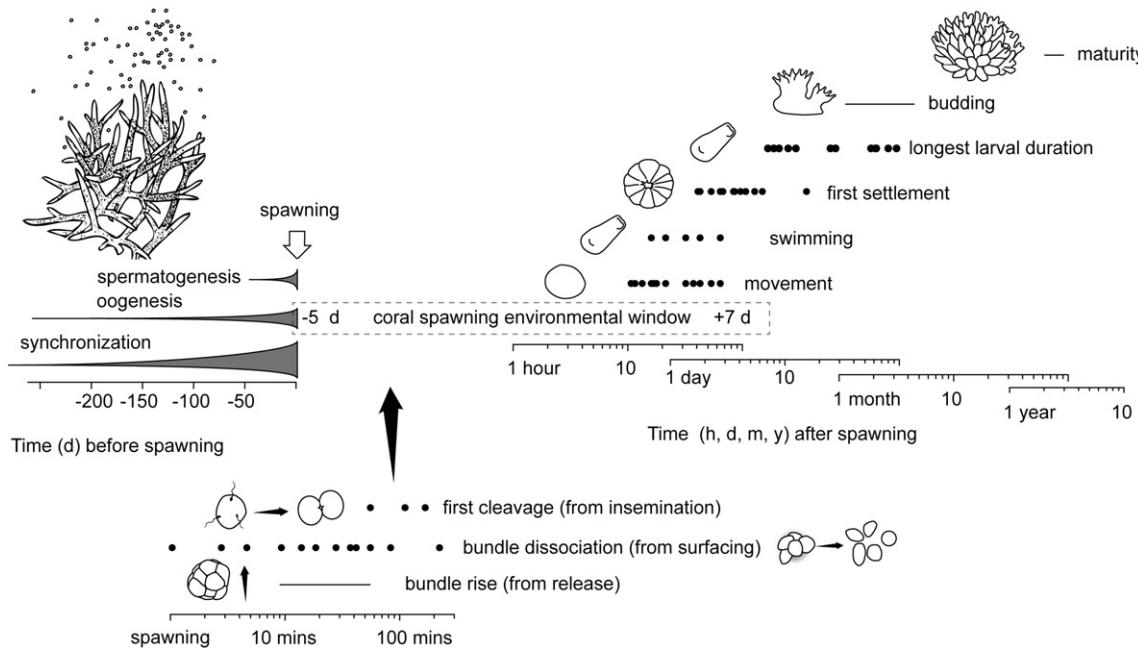
reduction in light reduced translocation of photosynthate from the algal symbionts to the host (Kojis and Quinn, 1984; Rinkevich, 1989; Tomascik and Sander, 1987). Since many corals species rely on their algal symbionts for a large proportion of energy required for growth and reproduction (Muscatine, 1990; Rinkevich, 1989), it is plausible that long-term shading by increased SSDs may impact upon gametogenesis. While no direct experiment have tested this directly, Shimoike et al. (1992) suggested reduced light and hence energy translocation could have accounted for the observed differences in spawning times of *Acropora* spp. in Okinawa which varied depending on whether parts of colonies were shaded by other acroporids. Similarly, Cantin et al. (2007) showed that chronic exposure of two broadcast spawning species (*Acropora tenuis* and *Acropora valida*) and a brooding species *Pocillopora damicornis* to photosystem II herbicide (diuron) that blocks photosynthesis caused reduced lipid levels (indicating less energy production). Polyp fecundity was subsequently reduced by 6-fold in *A. valida*, and both *A. valida* and *P. damicornis* were unable to spawn or planulate following long-term exposures.

These studies provide experimental evidence of links between reduced energy acquisition due to shading, inhibition of algal symbiont photosynthesis or by bleaching. Cause–effect pathways and modes of action could therefore include interference with algal photosynthesis in adults, larvae with symbionts and recruits (autotrophy reduction) and heterotrophic suspension feeding (heterotrophy reduction, see Houlbr  que and Ferrier-Pag  s, 2009) which would reduce energy for gametogenesis (Fig. 4). Other effects of high sediment deposition rates

include reduced energy from increased self-cleaning. A reduction in light and changes in light cues associated with elevated turbidity could disrupt synchronization of oogenesis or spermatogenesis (gametogenic asynchrony, Fig. 4).

#### 4. Spawning synchrony and egg–sperm bundle release

Synchronization of gametogenesis occurs progressively in a population as development proceeds, culminating in the co-ordinated spawning of mature gametes. Overall spawning synchrony and gamete release is likely to be co-ordinated by a cascade of environmental variables such as temperature, seasonal solar insolation, wind speeds, monthly lunar or tidal cycles, and diel light cycles which are operating on increasingly finer time scales and acting alone or in combination to harmonize reproduction (Babcock et al., 1986; Harrison and Wallace, 1990; Oliver et al., 1988; Rosser, 2013; Van Woesik, 2010; Van Woesik et al., 2006). The final sequence of events are complex, starting with the egg and sperm being packaged together in a mucous-layer to form an egg–sperm bundle (Okubo and Motokawa, 2007; Padilla-Gamino et al., 2011). Just prior to spawning the bundles are moved into the oral disc area where they become visible in the pharynx, this is referred to as ‘setting’ (Babcock et al., 1986; Wallace, 1985b). The release of bundles varies between species, but typically occurs within minutes to hours of setting (Babcock et al., 1986; Fukami et al., 2003; Levitan et al., 2004; Toh et al., 2012; Van Veghel, 1994). Spawning usually occurs through the extrusion or forcible ejection of the bundles from the mouth (Babcock et al., 1986) although



**Fig. 3.** Durations of each of the life-cycle phases depicted in Fig. 1, from broadcast spawning species listed in Table 1. Maturity, oogenesis and spermatogenesis estimates are from (Harrison and Wallace, 1990) and (Wallace, 1985b) and bundle rise rates are estimated from 1–15 m depth based on a vertical rise rates of  $8.3 \text{ mm s}^{-1}$  (Levitin et al., 2004). Most studies describing cleavage were conducted ex-situ and insemination was controlled and therefore cleavage is given as the time from insemination, not spawning. Movement is defined as any observable motion of the larvae associated with ciliation, and swimming is active movement in a given direction although detailed time-courses have not always been well-defined. Settlement is estimated from those studies where appropriate settlement cues have been used and associated with binding of the larvae to a substrate and not necessarily metamorphosis. Studies where references to timing were too vague, or studies where settlement cues were either not provided or not specified, were not included in the analyses. Extended larval durations are based on (Figueiredo et al., 2013; Harii et al., 2007; Harrison, 2006; Miller and Mundy, 2003; Nishikawa et al., 2003; Nozawa and Harrison, 2002; Nozawa and Harrison, 2005, 2008; Suzuki et al., 2011; Toh et al., 2012). The present coral spawning environmental window in Western Australia is from 5 days before to 7 days after the predicted start of coral spawning (i.e. for 12 days).

extrusion through temporary openings in the tentacles has been seen with some brooding (Duerden, 1902), and broadcast spawning species (Vermeij et al., 2010b).

Babcock et al. (1986) described the spawning of 17 species of corals within an hour of each other on the same day. Although the release of the egg–sperm bundles can be highly synchronous, different species can spawn between one and eight days after the full moon with peak spawning on the third to sixth night. Similarly, mass spawning in *Acropora* in Okinawa, Japan occurs from three days before up to seven days after the full moon (Hayashibara et al., 1993) and some species can spawn on multiple nights. Importantly, different species also have different release times from 10 min after sunset (i.e. *A. tenuis*) to ~3.5 h after sunset (i.e. *Platygyra sinensis*). The release times for these species may be within 15 min of each other between years (Babcock et al., 1986). Subtle differences in the timing of the arrival of egg–sperm bundles at the surface could be a mechanism for reproductive isolation i.e. a prezygotic isolating barrier to prevent or reduce hybridization between closely-related species (Fukami et al., 2003; Knowlton et al., 1997; Levitan et al., 2004; van Oppen et al., 2002; Willis et al., 2006).

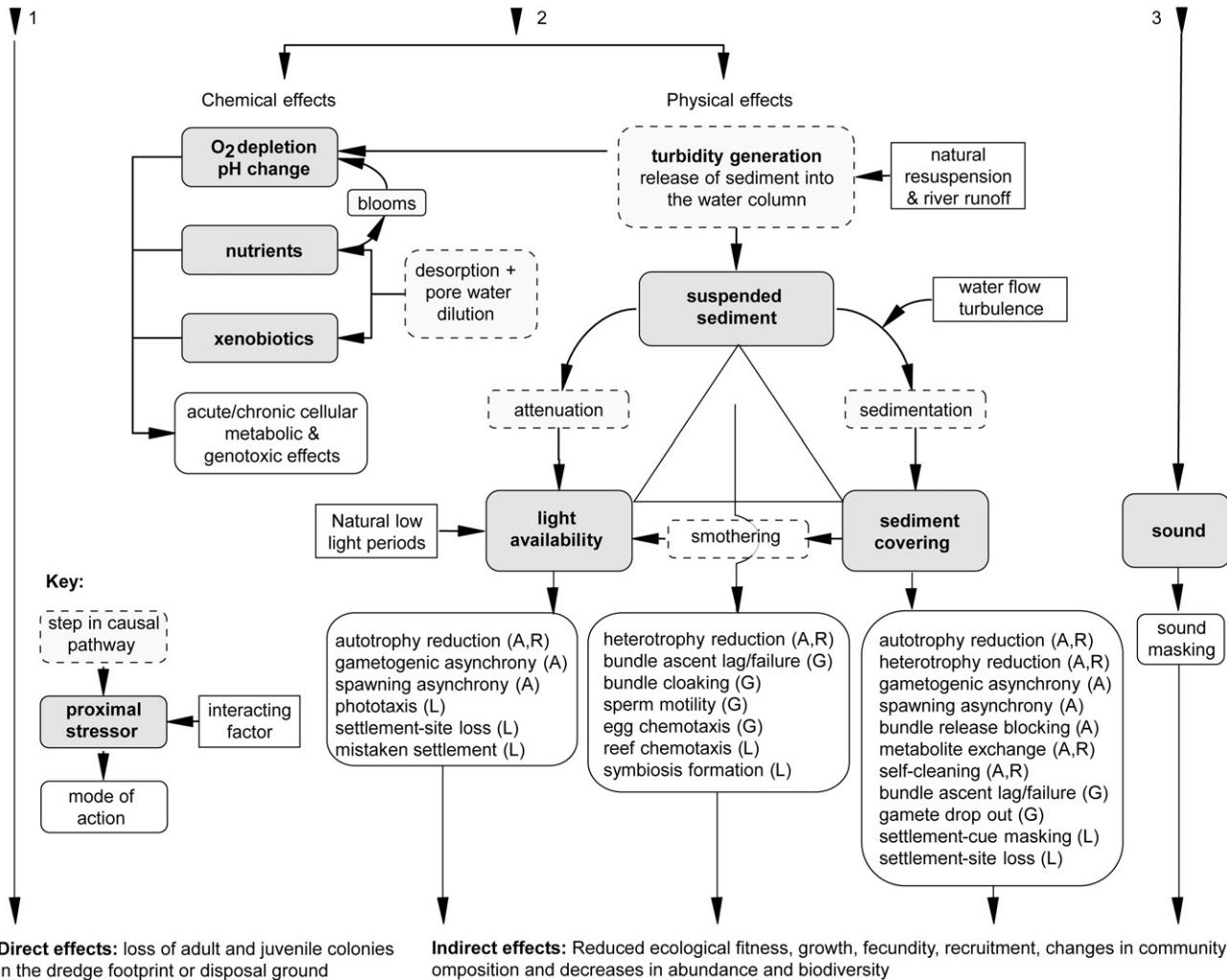
Jokiel et al. (1985) showed lunar periodicity in the brooding species *P. damicornis* is entrained by cyclic variation in night-time irradiance, while Gorbunov and Falkowski (2002) demonstrated expansion and contraction behavior of polyps from several coral species in response to moonlight and that the response was not related to photosynthetic activity of the algal symbionts. Subsequently, Levy et al. (2007) reported the presence of cryptochromes (CRYs), blue-light sensing photoreceptors in the ectoderm of both larval and adult *Acropora millepora* and coral rhodopsin-like genes have been described from *A. millepora* larvae (Anstil et al., 2007). Entrainment of corals by the lunar cycle results in the synchronization of spawning to within a few nights for most coral species, but the ultimate trigger for gamete release seems to be related to light (period after sunset) (Babcock et al., 1986; Harrison et al., 1984).

In the natural environment, egg–sperm bundle release is relatively consistent for each species at a given location; however, spawning can be accelerated or delayed. Delays can be induced by keeping corals in extended light periods (Harrison et al., 1984; Hayashibara et al., 2004). Conversely, corals can be induced to spawn early by placing corals in darkness during the day or by shortening the photoperiod (Babcock, 1984; Hunter, 1988; Knowlton et al., 1997). Brady et al. (2009) suggested the early shift was directly controlled by the solar cycle and not an entrained clock as *Montastraea* (= *Orbicella*) *franksi* spawned early following a single photoperiod manipulation. While these studies clearly suggest light is one of the proximal factors controlling the timing of spawning, they cannot explain the very tightly coupled spawning behavior within a single day i.e. to very discrete, 20–30 min periods when spawning occurs for each species. Possible cues include falling light intensities and the length of a period of darkness (Babcock, 1984; Hunter, 1988; Knowlton et al., 1997), and detection of the blue region of moonlight (Gorbunov and Falkowski, 2002). Tying these observations together Boch et al. (2011) and Sweeney et al. (2011) suggest that the presence, phase and position of the moon modulates the intensity and color (i.e. a blue shift) of downwelling irradiance during twilight, and that this is the final discrete, proximate trigger for the synchronous spawning of corals.

Buoyancy of invertebrate eggs and larvae is determined by lipid (i.e. wax esters, triglycerides and phospholipid) content (Chia et al., 1984) and coral eggs are very lipid-rich (Arai et al., 1993; Figueiredo et al., 2012; Harii et al., 2007, 2010; Padilla-Gamiño et al., 2013; Richmond, 1987; Wellington and Fitt, 2003). Consequently once released the egg–sperm bundles usually rise through the water column to the surface and form a slick (Fig. 1). Newly fertilized eggs of *Montastraea* (= *Orbicella*) *faveolata* have a vertical rise rate of  $1.8 \text{ mm s}^{-1}$  (Szamt and Meadows, 2006) and Levitan et al. (2004) recorded an average ascent rate of  $8.3 \text{ mm s}^{-1}$  for *Montastraea* (= *Orbicella*) *franksi* bundles. Although clearly dependent on depth, typically the time taken for the

**Source:** Marine and/or terrestrially derived igneous and/or siliciclastic and/or mixed biogenic subtidal and intertidal marine sediments

**Human activity:** Capital and maintenance dredging of: shipping channels, gas trunklines, berth pockets, turning basins, material offloading facilities  
dredge material (spoil) disposal • sand borrowing • aggregate mining • land reclamation • bed levelling • propeller wash • other marine infrastructure operations (marine dewatering)



**Fig. 4.** Conceptual model of the effects of dredging activity on the early life-history stages of corals including sources of sediments, dredging and dredging-related turbidity-generating activities (see text), as well as proximal stressors, interacting stressors are depicted along with modes of action and likely physiological and ecological responses (see text for explanation). G = gametes, L = larvae, R = recruits and A = adults.

egg–sperm bundles to rise through the water column to form the coral-spawn surface slick would be typically less than an hour (Oliver and Babcock, 1992; Van Veghel, 1994).

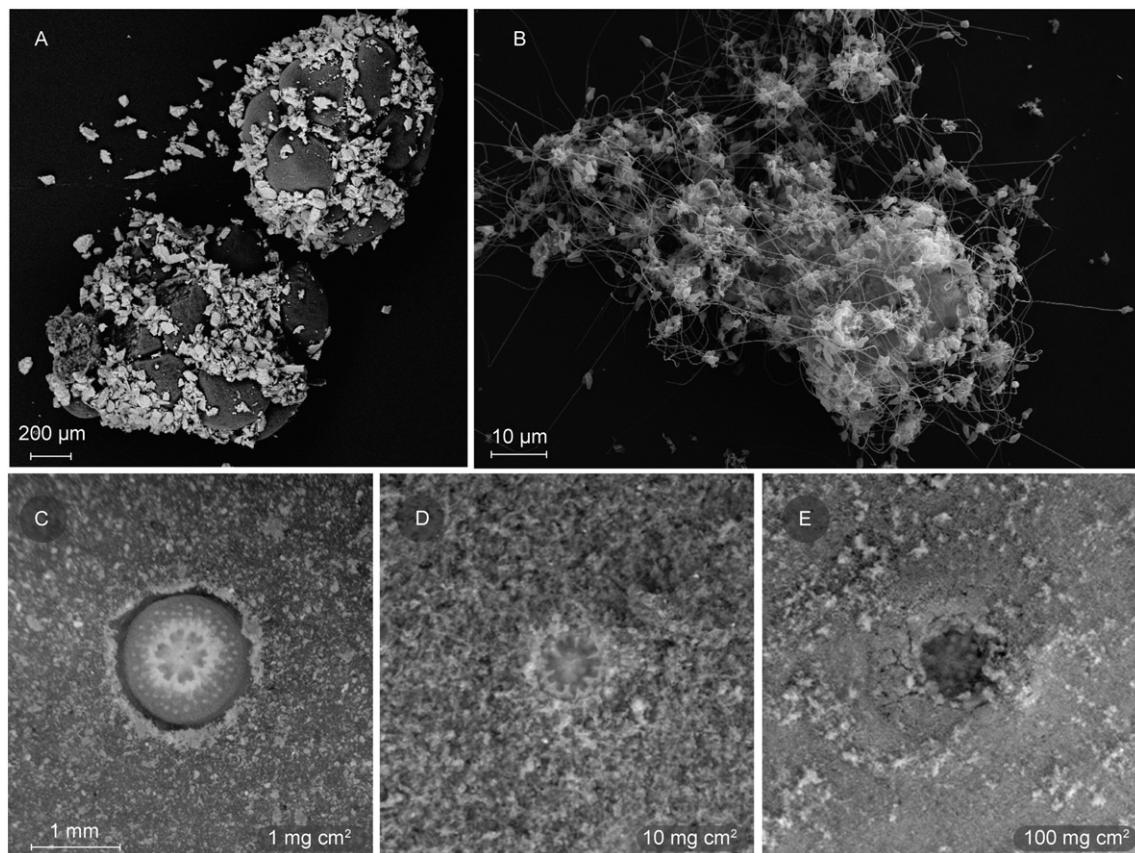
#### 4.1. Effects of sediment on spawning synchrony and egg–sperm bundle release

No studies have directly examined the effects of sediments on spawning but a range of plausible cause–effect pathways exist involving masking of synchronization cues by changes in light quantity and quality which could affect the timing of egg–sperm bundle setting and release processes (spawning asynchrony, Fig. 4). Such asynchronization has been demonstrated by shading colonies, showing the mechanism is probable (Brady et al., 2009; Levitan et al., 2004). This asynchronization could result in the un-coordinated arrival of the egg–sperm bundles on the surface. Sediment deposition and temporary smothering of corals could also interfere with egg–sperm bundle release (bundle release blocking, Fig. 4). Kojis and Quinn (1981a) described the stickiness of egg–sperm bundles of *Goniastrea australensis* and recent studies

(Ricardo unpublished data) have shown that sediments can directly bind to egg–sperm bundles of *Acropora nasuta* (Fig. 5A) and under conditions of high SSCs and could cause sinking of bundles or reduce the ascent rate following spawning (bundle ascent lag, Fig. 4). High rates of sedimentation could have a similar effect. As with asynchronous spawning, bundle ascent lag could also affect the co-ordinated arrival of egg–sperm bundles at the sea surface.

#### 5. Fertilization

At the surface the bundle dissociates releasing the eggs and sperm (Fig. 1). Reported times taken for the bundles to dissociate ranges from less than 5 min to more than 4 h, but the process is typically complete within an hour (Heyward and Collins, 1985; Padilla-Gamino et al., 2011; Richmond, 1997; Wolstenholme, 2004) (Fig. 3, Table 2). Wolstenholme (2004) noted that in *Acropora* sp. the time for bundle dissociation is consistently different for each of species (and morphs) and this could also be part of a mechanism for reproductive isolation.



**Fig. 5.** (A) Silt and clay sized sediment attached to the mucous-layer of an intact and a partially dissociated egg–sperm bundle of *Acropora nasuta*. Attachment of the negatively buoyant sediment to the bundles could reduce their buoyancy reducing ascent rate and at high concentrations even preventing them reaching the surface (Image: Gerard Ricardo). (B) Sperm from *Acropora tenuis* intertwined with silt and clay sized sediment particles. Sediments could act as a barrier and impediment to sperm movement and sediments with attached sperm could settle out of suspension potentially stripping them from the upper water column hence reducing egg–sperm contact time (Image: Gerard Ricardo). (C, D, E) Recently settled coral larvae (*Pocillopora actua*) 3 days h after exposure to single sediment deposition event of  $1 \text{ mg cm}^{-2}$ ,  $10 \text{ mg cm}^{-2}$  and  $100 \text{ mg cm}^{-2}$  of fine sediments (median grain size of  $\sim 50 \mu\text{m}$ ), showing the successful clearance of sediments from the polyp's surface under  $1 \text{ mg cm}^{-2}$ , but a progressive smothering of the polyps at higher concentrations (Image: Gerard Ricardo).

Since eggs are positively buoyant they remain on the surface, while the negatively buoyant sperm sink in the water column and became diluted at depth (Padilla-Gamino et al., 2011). Scleractinian eggs range in size from 400–800  $\mu\text{m}$  in Acroporidae and Mussidae, 300–500  $\mu\text{m}$  in Faviidae and Pectiniidae and 100–250  $\mu\text{m}$  in Agariciidae, Fungiidae and Pocilloporidae (Harrison and Wallace, 1990). Mature anthozoa sperm are typically  $\sim 50 \mu\text{m}$  long with a head diameter of 1–3  $\mu\text{m}$  (Hagedorn et al., 2006; Harrison, 1985; Steiner, 1991; Steiner and Cortés, 1996) as compared with silt sized sediments which range from 4–62.5  $\mu\text{m}$  based on the Udden–Wentworth (Wentworth, 1922) US standard classification scale of sediment (see Fig. 5B).

Fertilization in broadcast coral species occurs when the eggs and sperm dissociate from the bundle and become viable. This usually takes place at the surface or in the upper water column (Fig. 1). Heyward and Babcock (1986) noted for many corals (including several faviids) final maturation, division of the oocytes and the release of polar bodies occurred 15–30 min after spawning (see also Okubo and Motokawa (2007)). Consequently, it seems unlikely that the eggs are fertile until sometime after release from the bundles. For the sperm, Oliver and Babcock (1992) suggest they are also inactive when highly concentrated within the egg–sperm bundles at the time of spawning and become capable of full activity during the early stages of fragmentation of the bundles.

Morita et al. (2006) showed that sperm of *Acropora digitifera*, *Acropora gemmifera* and *A. tenuis* become activated when in close ( $<300 \mu\text{m}$ ) proximity to conspecific eggs but not eggs of different species. Coll et al. (1994) described substances extracted from eggs of *Montipora digitata* that activated and attracted sperm, while, Morita

et al. (2006) also described how sperm flagellar motility decreased when they came close to eggs where many sperm had already attached to the egg surface. These observations suggest the presence of sperm activation, attraction, chemotaxis (orientation with respect to a chemical concentration gradient) and suppressor(s), and a mechanism to prevent polyspermy given that eggs of corals do not have fertilization membranes (Babcock and Heyward, 1986; Oliver and Babcock, 1992).

First cleavage in laboratory studies generally occurs from  $<1$  h–6 h following fertilization (Fig. 3, Table 2) and the capacity for fertilization decreases with time, falling rapidly  $>1.5$  h after spawning in *M. digitata* (Oliver and Babcock, 1992), 2 h after spawning in *Montastrea annularis* species complex (Levitin et al., 2004),  $>3$  h in *Platygyra sinensis* (Oliver and Babcock, 1992),  $>5$ –6 h after spawning in *M. digitata*, *A. tenuis*, *Goniastrea aspera* and *Goniastrea favulus* (Heyward and Babcock, 1986), and *A. millepora* (Wallace and Willis, 1994; Willis et al., 1997). However, the majority of these fertilization studies were conducted in the laboratory (in vitro) (Table 1), without the natural dilution factors such as diffusion, advection and sinking of the sperm. Dilution of sperm in the field is likely to significantly impact on the length of the fertilization window and Omori et al. (2001) suggests that the in situ fertilization is unlikely as little as 1 h after spawning.

### 5.1. Effects of sediment on fertilization

The earliest study of the effects of sediment on fertilization was conducted with *A. digitifera* exposed to high sediment concentrations ( $1280 \text{ mg L}^{-1}$ ) at a low (28.5 ppt) salinity (Richmond, 1996; Richmond, 1993). Fertilization was much lower in the experimental

**Table 1**

Studies of the effects of sediments on aspects of the reproductive life-cycle of corals.

Study	Species	Particle size ( $\mu\text{m}$ )	Contaminant screening	Dose-response relationship
<i>Gametogenesis and reproductive synchrony</i>				
Tomascik and Sander (1987)	<i>Porites porites</i>	Not quantified	Nutrients only	Mean number of larvae per $\text{cm}^2$ of coral planulating <i>Acropora palifera</i> in Papua New Guinea, in shallow, turbid water sites was consistently half the value than at the clear water sites
Kojis and Quinn (1984)	<i>Acropora palifera</i>	Not quantified	None	Reduction in reproductive activity in <i>Porites porites</i> in Barbados along an increasing eutrophication gradient
Padilla-Gamiño et al. (2014)	<i>Montipora capitata</i>	Not quantified	None	No differences in gamete production in <i>Montipora capitata</i> in Hawaii between areas with different sediment trap accumulation rates.
<i>Fertilization</i>				
Gilmour (1999)	<i>Acropora digitifera</i>	50–200 $\mu\text{m}$	Metals	Effects of sediments collected from a terrestrial dredge spoil ground measured at 50 $\text{mg L}^{-1}$ and 100 $\text{mg L}^{-1}$ (measured concentrations)
Humphrey et al. (2008)	<i>Acropora millepora</i>	<63 $\mu\text{m}$ (Measured)	Metals and nutrients	Dose-response relationships established for % fertilization versus SSC over a range from 4–1024 $\text{mg L}^{-1}$ and an LOEC established at 100 $\text{mg L}^{-1}$ for a range of sediment types
Erfemeijer et al. (2012b)	<i>Pectinia lactuca</i>	Not quantified	Not quantified	Reduction at 43 $\text{mg L}^{-1}$ and significant reduction at 169 $\text{mg L}^{-1}$ (nominal concentrations) tested against a reference sample of 6 $\text{mg L}^{-1}$
<i>Embryogenesis and larval development</i>				
Gilmour 1999	<i>Acropora digitifera</i>	50–200 $\mu\text{m}$	Metals	No effects at concentrations of 100–150 $\text{mg L}^{-1}$
Humphrey et al. (2008)	<i>Acropora millepora</i>	<63 $\mu\text{m}$ (Measured)	Metals and nutrients	No effects at concentrations up to 200 $\text{mg L}^{-1}$
<i>Settlement and metamorphosis</i>				
Hodgson (1990)	<i>Pocillopora damicornis</i>	Sand 12% Silt 67% Clay 21%	None	Planulae settlement was markedly reduced where there was a layer of sediment <1 mm thickness
Babcock and Davies (1991)	<i>Acropora millepora</i>	Fine sand and silt	None	Reduced settlement at sediment traps accumulation rates of ~3 (LOEC), 6–7 and 110–325 $\text{mg cm}^{-2} \text{ day}^{-1}$ measured using sediment traps as compared with controls at 0.5 $\text{mg cm}^{-2} \text{ day}^{-1}$ (NOEC)
Babcock and Smith (2002)	<i>Acropora millepora</i>	90% <63 $\mu\text{m}$	None	Settlement lower in sediment treated areas (1.9–11.7 $\text{mg cm}^{-2} \text{ day}^{-1}$ ) scrubber pad accumulation rates as opposed to control sites where sedimentation rates were 0.8–1.3 $\text{mg cm}^{-2} \text{ day}^{-1}$
Te (1992)	<i>Pocillopora damicornis</i>	Unspecified	None	0, 10, 100, and 1000 $\text{mg L}^{-1}$ (NOEC) concentrations with no significant difference in settlement between control and highest concentrations tested but polyp bailout in 100 and 1000 $\text{mg L}^{-1}$ concentrations
Gilmour (1999)	<i>Acropora digitifera</i>	50–200 $\mu\text{m}$	Metals	50 $\text{mg L}^{-1}$ and 100 $\text{mg L}^{-1}$ (measured concentrations) tested against a reference of >1 $\text{mg L}^{-1}$
Perez et al. (2014)	<i>Pocillopora damicornis</i>	<63 $\mu\text{m}$	None	No settlement on surfaces >0.9 $\text{mg cm}^{-2}$
<i>New recruits</i>				
Babcock and Smith (2002)	<i>Acropora millepora</i>	90% <63 $\mu\text{m}$	None	Settlement lower in sediment treated areas (1.9–11.7 $\text{mg cm}^{-2} \text{ day}^{-1}$ ) scrubber pad accumulation rates as opposed to control sites where sedimentation rates were 0.8–1.3 $\text{mg cm}^{-2} \text{ day}^{-1}$

treatment than controls (0.45  $\mu\text{m}$  filtered seawater at 34 ppt and no sediment); however those results could be partially due to osmotic effects since later experiments showed similarly low fertilization rates at low salinity without sediments (see also Humphrey et al., 2008).

Several studies have examined the effects of suspended sediment on fertilization in *A. digitifera* (Gilmour, 1999), *A. millepora* (Humphrey et al., 2008), and *Pectinia lactuca* (Erfemeijer et al., 2012b), using sediments collected from terrestrial dredge spoil grounds and surficial sub-tidal sediments collected from a range of locations including pristine and contaminated sites (Table 1).

The effects of suspended sediments on coral fertilization varied considerably in these studies. Some of the differences may be due to uncertainty in the amount of sediments suspended over the duration of the exposures. In the most sensitive study, Gilmour (1999) placed hundreds of grams of sediment in a container and used aeration from aquarium pumps channelled through a pipette to re-suspend the fine-grained sediment from the container floor to the desired levels in the water column. Recent attempts to create uniform suspensions of sediments using the same techniques have not been successful and new techniques are currently being developed (Ricardo unpublished).

Fertilization is known to be one of the most vulnerable life-history stages to toxicants, and some of the variation between studies could be associated with contaminants and genotoxic effects. Other possible

cause-effect pathways lie with the binding of nutrients and micro-organisms, potentially forming 'sticky' particles that may attract and capture coral sperm. It is notable that the clean aragonite sediments used by Humphrey et al. (2008) did not cause any measurable effect on fertilization at 1000  $\text{mg L}^{-1}$  as compared to the potentially contaminated sediments collected from beside a nearshore, operational dock where affects were observed at 100  $\text{mg L}^{-1}$ . Similarly, sediments in the study of Erfemeijer et al. (2012b) were collected from Singapore waters which are likely to be contaminated by a range of pollutants, including potentially toxic persistent organic pollutants (Wurl and Oubbard, 2005).

Another source of the variability between the studies could be methodological differences especially in sperm concentrations. So far studies have used only a single sperm concentration but if suspended sediments limit the available sperm for fertilization, then the fertilization rate can be highly dependent on the sperm concentration used, masking effects at very high in vivo sperm concentrations and exacerbating effects at low sperm concentrations (Marshall, 2006). The experiments so far have typically used a single sperm concentration and while the use of a single concentration is quick and convenient, future studies need to consider a range of sperm concentrations since fertilization success is proportional to sperm-egg contact and increases with increasing sperm concentration (Iguchi et al., 2009; Marshall, 2006; Oliver and

Babcock, 1992). Different techniques and metrics have been proposed to address this and other issues, including use of a number of sperm concentrations, the use of a standard sperm–egg contact times, optimizing sperm and egg concentrations for each species to maximize the sensitivity of an assay (Oliver and Babcock, 1992; Omori et al., 2001), and using sperm of multiple corals (Marshall, 2006).

The mechanism whereby sediments effect fertilization is unknown and could include physical effects on egg/sperm interactions through affecting sperm activation, effects on motility, and entry and attraction. As with processes leading to asynchrony, these may serve to reduce egg–sperm interactions and will ultimately affect recruitment. Humphrey et al. (2008) and Erfemeijer et al. (2012b) speculated that sediments may block sperm entry to the egg via the micropyle, and while these structures are found in fish, insects and cephalopods, they have not been described yet for coral eggs. Gilmour (1999) observed unusual clustering or aggregation of *A. digitifera* eggs on the water surface in sediment-treated samples. These observations are similar to those made with Pacific herring where sediments attach and aggregate eggs and embryos in the early post-fertilization period, remaining there for the duration of embryonic development (Griffin et al., 2009).

Other possible pathways include attachment of sediment to the mucus-layer of the egg–sperm bundles preventing or delaying break up (bundle cloaking in Fig. 4). Silt sized sediments (4–62 µm) could also interfere with sperm movement decreasing sperm–egg interactions (sperm motility in Fig. 4) and possibly by masking activation and attraction cues from the eggs (egg chemotaxis in Fig. 4). As with the effects on egg–sperm bundles, attachment of sediments to sperm could cause them to sink (sperm drop-out in Fig. 4, Fig. 5B, C) and high sedimentation rates could accelerate this process.

## 6. Embryogenesis and larval development

The term embryo is used here to describe the early development phase of fertilized eggs up until the stage where the epidermis begins to differentiate and cilia form, at which stage the developing propagule is termed as larvae (Ball et al., 2002; Harrison and Wallace, 1990). Babcock and Heyward (1986) described embryogenesis in 19 species of corals from initial cleavage to 10 days afterwards including settlement and metamorphosis. Detailed time-courses in embryogenesis in gamete spawning *Acropora*, including the appearance of polar bodies, development of the zygote from cleavage, morular and blastula stage and gastrulation have been given in Hayashibara et al. (1997), Okubo and Motokawa (2007), Okubo et al. (2008, 2013) and Ball et al. (2002) and used to develop the stylized life-cycle in Fig. 1.

Fertilization and the initial stages of embryogenesis occur at the sea surface and upper water column (Fig. 1). The positive buoyancy in eggs and recently fertilized embryos during the first few days would enhance passive dispersal by currents, but an important feature of embryogenesis is a general decrease in buoyancy (Babcock, 1984; Figueiredo et al., 2012; Harrison et al., 1983; Wilson, 1888). Motility is typically first observed by 1–2 days after fertilization and active swimming after 2–3 days, although more rapid development have been recorded in some species such as *P. lactuca* (Fig. 3, Table 2). These observations on movement and swimming in the laboratory are supported by studies of coral slicks at sea (Babcock and Heyward, 1986) and the downward movement of larvae could be assisted by swimming (Harii et al., 2007; Tay et al., 2011). Willis and Oliver (1988) observed larval numbers increasing under the surface after 24 h and after five days the larvae were distributed evenly through the water column. The decrease in buoyancy and onset of motility results in a breakup of the coral surface spawn slicks, consistent with aerial observations that the slicks were visible for 1–2 days (Oliver and Willis, 1987).

Once motile, the planulae change from a barrel to a pear/elongate/spindle/tear drop shape (Hayashibara et al. (1997)) and are active swimmers, spiraling along their principal axis exhibiting a range of geotactic and negative and positive phototactic responses which contribute

to their ultimate settlement and attachment location (Lewis, 1974). Hodgson (1985) suggested evidence of vertical migration, with coral larvae residing near the surface at night and moving to several meters depth during the day. When swimming in the water column the downward navigation of the planulae in two brooding coral species (*Agaricia tenuifolia* and *Porites astreoides*) can be cued by seawater collected from the reef i.e. involves water-borne signals (Gleason et al., 2009). Vermeij et al. (2010a) also showed that planktonic phase larvae of *Montastraea faveolata* respond to underwater reef sounds such as fish calls and grunts and the snapping of shrimps by swimming to the substratum.

Non-symbiotic coral larvae are lecithotrophic and acquire energy endogenously from the parent generation and the rich lipid content is a plausible, primary energy source (Arai et al., 1993; Harii et al., 2007; Richmond, 1987; Wellington and Fitt, 2003). This is consistent with the slow decrease in the lipid content in *P. damicornis* (Richmond, 1987, 1997), *A. tenuis* (Harii et al., 2007), *P. damicornis* and *M. digitata* (Harii et al., 2010) during the planktonic phase, linked to loss of buoyancy. However also associated with the energy status of the larvae, and one of the most critically important events in the early life history stages, is the acquisition of photosynthetic, symbiotic dinoflagellate microalgal symbionts (*Symbiodinium* spp. = zooxanthellae) (discussed further below under metamorphosis). Species of the genus *Acropora* were believed to only uptake algae after metamorphosis (Babcock and Heyward, 1986; Babcock, 1988; Harrison and Wallace, 1990) but many recent studies have now shown that *Acropora* larvae can form symbioses at the larval stage (van Oppen, 2001; Baird et al., 2006; Adams et al., 2009; Harii et al., 2009; Baird et al., 2010; Cumbo et al., 2013). Richmond (1981) showed that between 13 and 27% of carbon fixed by *Symbiodinium* in *P. damicornis* larvae is translocated to the host, depending on light quality and temperature. This horizontal acquisition of symbiotic dinoflagellates at the larval stage or maternal inheritance in eggs has implications for the nutrition of the larvae, potentially increasing the length of the settlement-competency period and hence for dispersal.

### 6.1. Effects of sediment on embryogenesis and larval development

Gilmour (1999) and Humphrey et al. (2008) examined effects of sediments on early embryonic development in *A. digitifera* and *A. millepora* and showed no effect at the highest concentrations tested (100–150 and 200 mg L<sup>-1</sup>, respectively) (Table 1). Studies on the effects of sediments on the subsequent development in larvae is limited to the work of Gilmour (1999) where, in contrast to the lack of effects on embryogenesis, significant effects were noted from 1.5–6.5 days after spawning at concentrations as low as 50 mg L<sup>-1</sup>. To undertake this study, larvae were incubated in rearing jars containing several hundred grams of sediment and tethered in situ to mooring buoys. The ends of the jars were covered with a 60 µm plankton mesh to allow water exchange and retain the sediments which were kept in suspension by natural agitation of the buoy and containers by wave motion. These types of experiments are uncontrolled in that sediment particles less than the mesh size are likely to be lost and water flow inside the container was likely to be minimal because of clogging of the mesh by sediment. Gilmour (1999) described these limitations and how the containers were regularly squeezed to facilitate water exchange, but how this did not remove all solid materials caught inside the mesh which resulted in the build-up of tissue debris and organic material. Build-up of dead material could also have been exacerbated by the comparatively high larval densities of ~15 mL<sup>-1</sup> which may increase mortality within the meshed containers (Negri unpublished results). Despite these considerable methodological limitations, the impact on survival of 50 mg L<sup>-1</sup> has been widely cited, including in several recent reviews (Erfemeijer et al., 2012a; Fabricius, 2005; Gleason and Hofmann, 2011) but should be validated under more reliable conditions.

There are a number of potential cause–effect pathways whereby dredging could negatively or positively affect the larvae while in the

**Table 2**

Timing information for egg–sperm bundle dissociation, first cleavage, movement, swimming and attachment/settlement, symbiosis formation and budding. Only studies that described the minimum time of a given developmental stage were included and only studies on broadcast spawners that meet the criteria discussed in the text.

Study	Species	Timing
<i>Bundle break-up/dissociation</i>		
Kojis and Quinn (1982)	<i>Favites abdita, Leptoria phrygia</i>	A few minutes to 1 h after reaching the surface
Babcock (1984)	<i>Goniastrea aspera</i>	30 min after reaching the surface
Hunter (1988)	<i>Montipora verrucosa, M. dilatata</i>	45–90 min
Shlesinger and Loya (1991)	<i>Favia favus, Platygryra lamellina</i>	10–20 min after spawning
Richmond (1997)	<i>Acropora digitifera</i>	10–40 min
Hayashibara et al. (1997)	<i>Acropora hyacinthus, A. nasuta, A. florida</i>	Immediately
Wolstenholme (2004)	<i>Acropora gemmifera, A. samoensis</i>	5–30 min
	<i>Acropora humilis</i>	1–4 h
	<i>Acropora monticulosa</i>	30–60 min
	<i>Acropora digitifera</i>	5–15 min
Szamt and Miller (2006)	<i>Montastraea faveolata, Acropora palmata</i>	40 min, >60 min
Toh et al. (2012)	<i>Acropora hyacinthus, Pectinia lactuca</i>	20–30 min
<i>First cleavage</i>		
Babcock and Heyward (1986)	<i>Goniastrea favulus, G. aspera, Montipora digitata, Platygryra sinensis</i>	2 h and ~100% fertilization at 5–7 h
Shlesinger and Loya (1991)	<i>Favia favus, Platygryra lamellina</i>	~3 h after spawning
Hayashibara et al. (1997)	<i>Acropora hyacinthus, A. nasuta, A. florida</i>	2–6 h after fertilization
Okubo and Motokawa (2007)	<i>Acropora digitifera, A. intermedia, A. hyacinthus, A. solitaryensis, A. tenuis</i>	Within 2 h after fertilization
Okubo et al. (2008)		
Gilmour (1999)	<i>Acropora digitifera</i>	1.5–3 h after fertilization
Hirose et al. (2008)	<i>Acropora microphthalma, A. nobilis</i>	2 h after spawning more than 90% began cleavage
Okubo et al. (2008)	<i>Acropora intermedia</i>	2 h after spawning
Erfemeijer et al. (2012a,b)	<i>Pectinia lactuca</i>	~1 h after fertilization
<i>Movement</i>		
Kojis and Quinn (1981a)	<i>Goniastrea australensis</i>	Ciliated in <2 days
Babcock (1984)	<i>Goniastrea aspera</i>	Some movement 24–36 h after spawning
Harrison et al. (1984)	<i>Acropora hyacinthus, A. muricata, A. tenuis, A. millepora, A. tenuis, Goniastrea aspera, G. favulus</i>	1.5 day
Babcock and Heyward (1986)	<i>Favia pallida, Goniastrea aspera, G. favulus, Montipora digitata, Platygryra sinensis</i>	24 h
	<i>Acropora muricata, A. millepora, Galaxea fascicularis, Goniopora lobata, Lobophyllia corymbosa, Montipora tuberculosa, Mycedium elephantotus, Paraclavarina triangularis, Pectinia alcicornis, P. paeonia</i>	Mobile when first observed at 36 h
Hayashibara et al. (1997)	<i>Favites complanata</i>	Mobile when first observed at 48 h
Schwarz et al. (1999)	<i>Acropora hyacinthus</i>	36 h
Gilmour (1999)	<i>Lobactis scutaria</i>	12 h after fertilization
Hayashibara et al. (2000)	<i>Acropora digitifera</i>	Most by 36 h
Miller and Mundy (2003)	<i>Acropora nasuta</i>	Second day after fertilization
Nozawa and Harrison (2005)	<i>Platygyra daedalea</i>	42 h
Nozawa and Harrison (2006)	<i>Goniastrea favulus</i>	48 h
Harrison (2006)	<i>Favites chinensis, Goniastrea aspera</i>	Mobile <24 h after spawning
Nozawa et al. (2006)	<i>Acropora muricata, A. valida</i>	Mobile when first observed at 3 days
Okubo and Motokawa (2007)	<i>Acropora longicyathus, A. hyacinthus</i>	2 days after spawning
Okubo et al. (2008)	<i>Acropora solitaryensis, Cyphastrea serailia, Favia favus</i>	48–72 h after spawning
Toh et al. (2012)	<i>Acropora digitifera, A. hyacinthus, A. intermedia, A. solitaryensis, A. tenuis</i>	36 h
Erfemeijer et al. (2012b)	<i>Acropora hyacinthus</i>	Within 48 h
Figueiredo et al. (2013)	<i>Pectinia lactuca</i>	18 h
	<i>Pectinia lactuca</i>	12–18 h after fertilization
	<i>Palauastrea ramosa</i>	8 h
Okubo et al. (2013)	<i>Danafungia horrida, Leptastrea purpurea</i>	12 h
	<i>Goniastrea aspera</i>	16 h
	<i>Goniastrea retiformis, Pachyseris speciosa, Platygryra daedalea, Porites austroliensis</i>	18 h
	<i>Echinopora lamellosa, Merulina ampliata, Montipora digitata</i>	24 h
	<i>Anacropora puertogalerae</i>	26 h
	<i>Physogyra lichtensteini, Plerogyra sinuosa</i>	30 h
	<i>Acropora gemmifera</i>	32 h
	<i>Acropora humilis, A. millepora, A. pulchra, A. valida</i>	36 h
	<i>Pavona decussata</i>	12 h after spawning
	<i>Oulastrea crispata</i>	13 h after spawning
	<i>Favites pentagona, Echinophyllia aspera</i>	15 h after first cleavage
	<i>Galaxea fascicularis, Goniastrea favulus</i>	18 h after spawning
	<i>Platygyra contorta, Phymastrea valenciennesi</i>	19 h after spawning
	<i>Favites abdita</i>	22 h after first cleavage
	<i>Dipsastrea speciosa</i>	24 h
	<i>Montipora digitata, M. hispida</i>	33 h after spawning
<i>Swimming</i>		
Babcock (1984)	<i>Goniastrea aspera</i>	48 h
Babcock and Heyward (1986)	<i>Acropora millepora, Favia pallida, Goniastrea aspera, G. favulus, Montipora digitata, Platygryra sinensis</i>	48 h
Hayashibara et al. (1997)	<i>Echinopora gemmacea</i>	36 h
Schwarz et al. (1999)	<i>Galaxea fascicularis, Goniopora lobata, Goniastrea retiformis, Lobophyllia hemprichii</i>	72 h
	<i>Acropora florida, A. hyacinthus, A. nasuta, A. secale</i>	72 h
	<i>Lobactis scutaria</i>	Within 24 h of fertilization

**Table 2** (continued)

Study	Species	Timing
<b>Swimming</b>		
Harii et al. (2007)	<i>Acropora tenuis</i>	48 h
Hirose et al. (2008)	<i>Acropora microphthalma, A. nobilis</i>	2 days after fertilization
Erftemeijer et al. (2012b)	<i>Pectinia lactuca</i>	By 18 h most larvae were rapidly motile
<b>Settlement</b>		
Babcock (1985)	<i>Goniastrea aspera, A. millepora, Platygryra sinensis</i>	After 4.5 days and the majority after 8–10 days
Babcock and Heyward (1986)	<i>Favia pallida, Platygryra sinensis, Goniastrea aspera, Galaxea fascicularis</i>	4.5 days
Harrison (1997)	<i>Goniastrea aspera, G. favulus, G. retiformis, Montipora digitata</i>	5 days
	<i>Acropora longicyathus</i>	Settlement 2–4 days and metamorphosis 3–4 days after spawning
Hayashibara et al. (1997)	<i>Acropora secale</i>	17–24 days
Heyward and Negri (1999)	<i>Acropora millepora</i>	5 days
Schwarz et al. (1999)	<i>Lobactis scutaria</i>	Larvae began to settle and metamorphose 5–14 days after fertilization
Hayashibara et al. (2000)	<i>Acropora nasuta</i>	3–4 days after fertilization peaking after 7 days
Nozawa and Harrison (2002)	<i>Platygyra daedalea</i>	Settlement 3–4 days and metamorphosis 4–6 days after spawning
Fabricius et al. (2003)	<i>Acropora willisae</i>	Settled and metamorphosized 3–5 days after spawning
Miller and Mundy (2003)	<i>Goniastrea favulus, Platygryra daedalea</i>	Settlement started at between 2.5 and 2.75 days
Nishikawa et al. (2003)	<i>Acropora tenuis</i>	4 days after spawning peaking 7 days after spawning
Nozawa and Harrison (2005)	<i>Favites chinensis</i>	1–2 days after spawning
Harrison (2006)	<i>Goniastrea aspera</i>	3–4 days after spawning
Harii et al. (2007)	<i>Acropora longicyathus, A. hyacinthus</i>	2–3 days after spawning
Hirose et al. (2008)	<i>Acropora tenuis</i>	3 days
Nozawa and Harrison (2008)	<i>Acropora microphthalma, A. nobilis</i>	2–16 days after fertilization
Okubo et al. (2008)	<i>Acropora muricata, A. valida</i>	First observed at 5–6, peaked at 7–8 days
Heyward and Negri (2010)	<i>Acropora intermedia</i>	7 days after spawning
	<i>Acropora millepora, Fungia repanda, Symphyllia recta A. spathulata</i>	4 days after spawning
Suzuki et al. (2011)	<i>Acropora spp.</i>	3–4 days after spawning
Tay et al. (2011)	<i>Pectinia lactuca, Platygryra sinensis</i>	Commencing 2–5 days after spawning but 80% settled by 5–8 days
Toh et al. (2012)	<i>Acropora hyacinthus</i>	Peak settlement 3 and 6 days day after spawning respectively
	<i>Pectinia lactuca</i>	>50% settled by 1.7 days after fertilization
Figueiredo et al. (2013)	<i>Acropora gemmifera, A. humilis, A. millepora, A. valida, Goniastrea retiformis, Platygryra daedalea</i>	Starting at 3 days and >50% by 4 days after fertilization
Graham et al. (2013)	<i>Acropora tenuis</i>	~Metamorphosis 3–6 days from spawning
Okubo et al. (2013)	<i>Favites pentagona</i>	A few were competent to settle as early as 4 days after spawning
	<i>Favites abdita</i>	Started swimming at about 15 h
Dixson et al. (2014)	<i>Pseudosiderastrea tayamai</i>	Started swimming at about 15 h
	<i>Acropora millepora, A. nasuta, and A. tenuis</i>	3 days after spawning
		6–7 days after spawning
<b>Symbiosis</b>		
Babcock (1985)	<i>Acropora millepora, Goniastrea aspera, Platygryra sinensis</i>	Between 5 and 10 days after settlement
Babcock and Heyward (1986)	<i>Acropora millepora, Goniastrea favulus, Platygryra sinensis</i>	Sometime within 13 days after settlement
Hayashibara et al. (1997)	<i>Acropora microphthalma, A. nobilis</i>	16 and 30 days after settlement
Hayashibara et al. (1997)	<i>Acropora florida, A. hyacinthus, A. nasuta</i>	Established symbiosis after 30 days
Schwarz et al. (1999)	<i>Lobactis scutaria</i>	Symbionts phagocytosed as early as 3 days after fertilization
Harii et al. (2009)	<i>Acropora digitifera, A. tenuis</i>	5–6 days after fertilization
Graham et al. (2013)	<i>Acropora tenuis</i>	15 days after settlement
<b>Budding</b>		
Shlesinger and Loya (1991)	<i>Favia favus</i>	7–9 months after spawning
Hayashibara et al. (1997)	<i>Acropora secale</i>	2 months after fertilization
Graham et al. (2013)	s	~22 days after settlement

planktonic phase. Sound from dredging operations, high SSCs or reduced light levels associated with the high turbidity, could affect the macro-scale habitat selection, the orientation of the larvae in the water column and the downward movement towards the reef (i.e. sound masking, reef chemotaxis, phototaxis, in Fig. 4). High SSCs could also interfere with the algal acquisition process which is mediated by a feeding. The energetics of larvae may also be taxed by excessive particle removal (self-cleaning; Fig. 4) or avoidance and reductions in light quantity and quality would most likely negatively affect

photosynthesis in larvae that have acquired symbionts (autotrophy reduction in Fig. 4).

There are, however, a number of possible benefits of turbidity generating activities while embryos and larvae are in the water column. Resuspended sediments may include free-living algal symbionts increasing the chances of forming a stable symbiosis (see below). Light reduction could also reduce UV damage in embryos and oxidative stress in larvae that recently acquired symbionts in the planktonic phase and reduce losses to visual predators.

## 7. Settlement and metamorphosis

The pelagic larval phase ends with a gradual descent of the planulae from the surface and water column (i.e. planktonic stage) to a temporary demersal stage (Fig. 1). Subsequently there is a final, benthic stage, involving settlement and eventually permanent attachment (Fig. 1). Gleason and Hofmann (2011) have recently reviewed the ‘...dizzying array of abiotic and biotic factors, both positive and negative, that can determine whether a coral larva ultimately ends up on the reef as a new recruit...’.

Once near the seabed planulae exhibit thigmotactic ‘searching’ behavior, touching the substrate, temporarily ‘resting’, ‘creeping’ and ‘crawling’ over the surface before eventually attaching and settling (Fig. 1). Many studies have described similar processes with larvae of several brooding species and introduced the colloquial terms for the stages (Atoda, 1947a,b, 1951a,b; Duerden, 1902; Krupp, 1983; Wilson, 1888). Coral larvae lack the apical tufts found in some cnidarians but appear to have sensory cells in their aboral epidermis for substratum detection i.e. tasting surfaces for suitable cues. Vandermeulen (1974) described these sensory cells for larvae of *P. damicornis* as bearing a single flagellum and surrounded by a collar of microvilli. The nature of these cells and the location of chemoreception has recently been examined by Tran and Hadfield (2013) who showed that larvae *M. capitata* would not undergo metamorphosis if the first quarter of the aboral pole was removed. While suggesting sensory cells used in detecting cues are likely to be located there, much larger larvae of *P. damicornis* lacking the aboral pole were also able to settle and metamorphose. This indicated the cue-detecting cells could also be located along the sides of the body and there are differences between species in cue-detection.

Planulae of *A. nasuta* have 2 types of cnidae, a microbasic b-mastigophore nematocyst and a spirocyst (Hayashibara et al., 2000) that may aid attachment to surfaces. Spirocysts are known to be adhesive organelles in cnidaria and the discharged threads can link together in a fine web or meshwork (Mariscal et al., 1977). In *A. nasuta* the appearance of cnidae 3–4 days after fertilization coincides with the swimming phase and first attachment (Fig. 3), and a continued increase in numbers until 8 days after fertilization coincides with maximum settlement (Hayashibara et al., 2000). Okubo and Motokawa (2007) also observed an increase in numbers of spirocysts in a concave structure of the aboral region of developing *A. millepora* larvae. Hayashibara et al. (2000) suggested that the spirocysts were associated with attachment and Okubo and Motokawa (2007) proposed that the brim of the concave structure may sense the environmental signals for metamorphosis.

The settlement of mature planulae requires the presence of an appropriate substratum as well as chemical and/or biological cues and in some instances the presence of compatriots i.e. gregarious settling behavior (Birkeland et al., 1981; Duerden, 1902; Edmondson, 1929; Kojis and Quinn, 1981a; Puill-Stephan et al., 2012; Tran and Hadfield, 2011; Wilson, 1888). Baird et al. (2003) showed that settlement of larvae is much higher on artificial surfaces which had been conditioned (left in situ for 8 weeks) in the parental habitat suggesting species- and habitat-specific substratum cues (see also Suzuki and Hayashibara (2011)). Marine bacteria and biofilms are a potential source of the cues on some conditioned surfaces (Negri et al., 2001; Webster et al., 2004), however the settlement of some coral larvae is most powerfully initiated by the presence of various species of crustose coralline algae (CCA) (Golbuu and Richmond, 2007; Harrington et al., 2004; Morse et al., 1988). While chemical inducers from CCA are far more potent than all other factors affecting the settlement of *Acropora* spp. (Tebben et al., 2015), larvae often prefer to attach immediately adjacent to the CCA (Heyward and Negri, 1999; Szmant and Miller, 2006) which has an array of defenses including sloughing of surface cells and natural antifouling compounds protecting it from colonization (Harrington et al., 2004).

Following the searching/exploring stage the larvae settle, undergoing attachment by the aboral end, followed by contraction at the oral-aboral axis forming a flattened disc that eventually becomes subdivided radially by mesenteries (Ball et al., 2002) (Figs. 1, 5C). Metamorphosis involves a dramatic reorganisation and tissue remodeling creating the sessile primary polyp (Grasso et al., 2011; Hirose et al., 2008; Vandermeulen, 1974, 1975; Vandermeulen and Watabe, 1973). In particular the aboral ectoderm is transformed into the calicoblastic ectoderm, which is responsible for secretion of the coral skeleton, and the oral ectoderm is stabilized (Grasso et al., 2011). While metamorphosis in most invertebrate larvae is usually an irreversible process, at least one species, *P. damicornis*, can undergo reversible metamorphosis back into the planktonic form under conditions of environmental stress or energy constraint (Miller and Mundy, 2003; Richmond, 1985).

Many studies of recruitment patterns suggest that larvae can exhibit adaptive behavior and actively settle at sites where the light quality and quantity regime is optimum (Duerden, 1902; Edmondson, 1929; Lewis, 1974; Miller and Mundy, 2003; Mundy and Babcock, 1998). In shallow environments juvenile corals tend to be found on vertical sides and cryptically, on the undersides of surfaces of dead corals or artificially provided settlement media such as settlement plates (Babcock and Mundy, 1996; Bak and Engel, 1979; Birkeland, 1977; Duerden, 1902; Harriott and Fisk, 1987; Wallace, 1985a). On the underside of plates settlement is often in an aggregated distribution near the edge (Maida et al., 1994) and recruits eventually extend out from these cryptic habitats as they grow. These settlement patterns have been suggested to be due to avoidance of predation or herbivorous grazing, or avoidance of sediment deposition and algal biomass (Birkeland, 1977; Maida et al., 1994) or an interaction whereby filamentous algae traps more sediment. However, it has also been pointed out that the majority of the settlement studies have used settlement plates with smooth upper surfaces which lack sufficient surface rugosity to provide refuge for small corals (see Penin et al. (2010), Nozawa et al. (2011), Edmunds et al. (2014), Nozawa et al. (2011) and Penin et al. (2010)).

The cryptic recruitment pattern on settlement plates reverses with depth, and on a proportional basis more juvenile corals tend to be found settled on horizontal than vertical surfaces in deeper water (Birkeland, 1977; Birkeland et al., 1981; Rogers et al., 1984; Sammarco and Carleton, 1981; Wallace, 1985a). This pattern has been suggested to be due to reduced light intensities at depth (Bak and Engel, 1979) and can occur either through settlement behavior or post settlement mortality. Mundy and Babcock (1998) found that some deeper water corals preferred low intensity blue light, indicating that spectral light quality is also an important cue for the settlement response in deep-water corals. The cryptic settlement pattern could also be related to ultraviolet radiation (UVR, 280–400 nm), which can penetrate to considerable depths (>24 m) in tropical waters (Banaszak and Lesser, 2009). Larvae appear particularly sensitive to UVBR (280–329 nm) radiation and exposure reduces survivorship in the brooding (Gleason and Wellington, 1995) and broadcasting species (Wellington and Fitt, 2003). While Baker (1995), Kuffner (2001) and Gleason et al. (2006) recorded reduced settlement of larvae from some brooding species in response to UVR there were no impacts on larval survival. Cryptic settlement appears to represent a relatively straightforward mechanism of reducing UVR damage and maximizing survival during the very early stages of recruit establishment. Overall, settlement of coral larvae probably represents a balance between opposing selective pressures of access to adequate light for photosynthesis versus avoidance of UV damage and competition with algae, sediment, and grazers (Gleason and Hofmann, 2011).

The minimum competency periods for coral larvae varies considerably (Fig. 3, Table 2). Part of the variation could be due to differences in the experimental systems used to quantify the onset of competency—see Heyward and Negri (2010) for a reliable technique for some species. If critical factors which influence settlement were not optimized in laboratory-based experiments then this may have led to some of the

extended minimum settlement times reported in the early literature—for example 36 days in *Acropora hyacinthus* (Harrison et al., 1984) as opposed to 7 days (Okubo and Motokawa, 2007), and 16–22 days in *Acropora formosa* (= *Acropora muricata*) (Harrison et al., 1984) as opposed to 5–6 days (Nozawa et al., 2006). Furthermore, the length of the competency period is likely to be underestimated as *Acropora* spp. kept in low densities and in the absence of cues to induce settlement are still competent to settle at least 60 days post-spawning (Negri unpublished data; Graham et al., 2008).

Of those studies where appropriate settlement cues were used to examine attachment, the settlement starts to occur from a few days to two weeks after spawning (Connolly and Baird (2010), Table 2). Most studies have described initial settlement but several more recent studies have followed the time course over several weeks (Harrison, 2006; Nozawa and Harrison, 2005, 2008; Suzuki et al., 2011; Tay et al., 2011; Toh et al., 2012) including a recent in situ study (Suzuki et al., 2011). Larval settlement generally peaks between 4 and 10 days after spawning but extended settlement times have been shown lasting several months, having implications for long-distance dispersal and increased genetic connectivity between distant reefs (Nishikawa et al., 2003; Nozawa and Harrison, 2005).

Several studies with *A. hyacinthus*, *A. muricata*, *Acropora longicyathus*, *A. valida*, *Platygyra daedalea*, *Favites chinensis* and broadcast spawned *G. aspera* on the southern Great Barrier Reef and in Japan, have shown the ability of larvae to rapidly settle and attach, occurring a few days after spawning and a few days before they achieve competence and undergo metamorphosis (Harrison, 1997, 2006; Miller and Mundy, 2003; Nozawa and Harrison, 2002; Nozawa and Harrison, 2005, 2008). This precocious settlement behavior, occurring prior to developing full competence, could provide a mechanism for some larvae of broadcast spawning corals to remain on or near their natal reef, allowing some degree of self-seeding of local populations.

### 7.1. Effects of sediment on settlement

There have been many more studies of the effects of sediments on settlement of broadcast and brooding species than at any other stage (Table 1). These studies have substantiated the observation by Johannes (1970) that coral larvae are reluctant to settle in the presence of sediment (Table 1). In laboratory-based experiments several different techniques have been used and sediment loads causing effects qualitatively and quantitatively described. Qualitative descriptions include ‘... a conspicuous layer of sediment...’ (Babcock and Davies, 1991) or ‘... layer of sediment...’ (Gilmour, 1999). More quantitative assessments have included the use of sediment traps to assess sedimentation rates (i.e. Babcock and Davies, 1991) which are unreliable for this purpose (see Storlazzi et al., 2011). The most recent work of Perez et al. (2014) has quantified the effect more thoroughly, showing that *P. damicornis* larvae would not settle on surface covered with a fine (<63 µm) terrigenous sediment of as little as >0.9 mg cm<sup>-2</sup> or ~<80 µm thickness.

There are few field based studies examining the effects of sediment on settlement and of these Babcock and Smith (2002) showed the broadcast-spawning species *A. millepora* would not settle in silty environments. Manipulative field experiments are difficult, and in that particular experiment sediment was delivered using fine (90% <63 µm) terrestrial sediment consolidated into bricks placed beside settlement tiles. The bricks crumbled on submersion, distributing sediment in their immediate vicinity and onto nearby coral settlement plates. Sediment supply was continued by occasionally placing more bricks nearby over the next few months when possible. In this study sedimentation rates were estimated by attaching household scrubbing pads to the reef and the amount of sediment accumulating in these pads was weighed and expressed in terms of mg cm<sup>-2</sup> day<sup>-1</sup>. The study confirmed the laboratory-based experiments, where corals will not settle in silty environment, however, this type of experiment is highly uncontrolled due to the application of sedimentation rates determined by a

method that cannot provide reliable quantitative information on the downward flux of sediments (Thomas and Ridd, 2004, 2005; Storlazzi et al., 2011; Risk and Edinger, 2011).

Birrell et al. (2005) examined settlement of *A. millepora* larvae on dead coral substrata with or without sediments and algal turf. Sediments were manipulated by placing 50 cm<sup>3</sup> of very fine sediments (<15 µm) collected by filtering reefal water in 9 L containers and allowing the sediment to settle over the experimental substrata. Maximum settlement occurred where sediments and algae were absent but the sedimentation rates or sediment thickness of suspended sediment concentrations were not quantified.

The most likely cause–effect pathways related to settlement are associated with sediment deposition and changes in light. These studies demonstrate that larvae prefer not to settle in the presence of sediment films. Unconsolidated sediment could mask or cover settlement cues like CCA or may simply represent a negative tactile response (settlement cue masking in Fig. 4). The ultimate effect is a reduction of suitable (bare) horizontally oriented substratum for settlement. Coral larvae have a tendency to settle in small cracks and crevices and Te (1992) and Babcock and Davies (1991) showed that they would settle in confined experimental containers under sedimentation regimes if presented with sediment-free refuges. In the field however, these are also areas where sediments would naturally accumulate.

A reduction in light or change in spectral quality could reduce the available substratum for settlement by reducing the photic zone (settlement site loss, Fig. 4). Gleason et al. (2006) suggested that under reduced light, larvae could mistakenly settle in areas (i.e. shallower depths) where the average light conditions do not favor long term survival once water clarity returns to normal. Larvae would then have to adapt rapidly to potentially high PAR or UV conditions or undergo reverse metamorphosis or polyp bail out to survive. Turbidity-dredging events could also result in such ‘settlement mistakes’ (Fig. 4).

### 8. New recruits

Immediately after settlement and metamorphosis, the corals are typically <1 mm and visible only with a stereo microscope (Fig. 5D). Several recent studies have shown that despite their small size, heterotrophic feeding (zooplanktivory) occurs quite quickly after settlement, with 2-day old recruits of *A. hyacinthus* and *P. damicornis* capable of capturing and consuming live brine shrimp (*Artemia salina*) nauplii (Toh et al., 2013). *P. damicornis* recruits fed with brine shrimp grew faster and had much higher survival rates when transferred to the field than unfed recruits (Toh et al., 2014). Acroporid and pocilloporid recruits can grow at a rate of ~0.2 mm diameter a week (Schmidt-Roach et al., 2008), reaching 1 cm by about 1 year (Fig. 3) (Babcock, 1985).

The small size of the new recruits makes them particularly vulnerable to a range of factors including sediment smothering (see below) and overgrowth by algae, competition from conspecifics or other benthic organisms, and direct grazing by coral-feeding fish or incidental mortality from scraping herbivorous fish (Penin et al., 2010, 2011). High mortality rates (>90%) are well known in most free-spawning marine invertebrates (Gosselin and Qian, 1997) and similarly high rates are also common in corals. Babcock (1985) reported mortality rates of ~90% in juvenile *A. millepora* and ~70% in *G. aspera* and *P. sinensis* which had attached on slabs of coral skeleton and returned to the field. Using similar techniques Nozawa et al. (2006) reported post-settlement mortality rates of 88–100% over a 3-month period in five species of scleractinian corals initially settled onto slate plates for a few months then transferred to the field. Nozawa (2010) reported post-settlement mortality rates of 40–60% per month and a yearly rate of 85% in *Acropora solitaria* which had been settled onto plain surfaces of fiber cement boards then transferred to the field. Similarly high rates of post-settlement mortality have also been observed in many other studies (see Nozawa, 2010; Nozawa and Okubo, 2011; Ritson-Williams et al.,

2010; Suzuki et al., 2013; Szmant and Miller, 2006; Trapon et al., 2013a, b; Vermeij and Sandin, 2008).

In juvenile and adult corals their symbiotic algae provide photosynthetically fixed carbon to the host providing additional energy for respiration and growth (Lesser, 2004). The initial establishment of symbiosis in *Acropora* recruits involves an attraction step (of *Symbiodinium* to the recruits) and a subsequent selective uptake step, suggesting the operation of recognition systems by 2 weeks (Yamashita et al., 2014). *Symbiodinium* are usually acquired by the hosts in feeding, and ultimately phagocytosed into the endodermal cells (Colley and Trench, 1983; Fitt and Trench, 1983a, b). The majority (~80%) of broadcast spawning species acquire the *Symbiodinium* horizontally (Douglas, 1994) i.e. from a free-living reservoir (Baird et al., 2009). Notable exception are *Porites* spp. and *Montipora* spp. where zooxanthellae are maternally inherited i.e. vertical transmission, through follicle cells into the unfertilized eggs shortly (weeks to days) prior to maturation (Babcock et al., 1986; Heyward and Collins, 1985; Kojis and Quinn, 1981b). In contrast, only about 15% of brooders acquire zooxanthellae from the environment (Baird et al., 2009). *Symbiodinium* ultimately reside in the endodermal tissues (Muscatine, 1990) of juveniles and adults at densities of typically one but up to six algae per host cell (Muscatine et al., 1998).

Forming the symbiosis enhances deposition of the skeleton in the well-known phenomenon of light-enhanced (DCMU-sensitive) calcification (Chalker and Taylor, 1975; Kawaguti and Sakamoto, 1948). Juvenile *A. digitifera* that have acquired algal partners calcify much faster than algal-free aposymbionts (Inoue et al., 2012; Tanaka et al., 2013) and the onset of the symbiosis is crucial for the energetic process of budding in newly settled *A. tenuis* recruits (Graham et al., 2013; Little et al., 2004).

Coffroth et al. (2006) successfully inoculated asymbiotic octocoral polyps (*Briareum* sp.) establishing an important step that some of the free-living *Symbiodinium* were capable of forming a symbiosis. Adams et al. (2009) subsequently established this for hard corals, showing aposymbiotic coral larvae acquired sediment-associated *Symbiodinium* spp. quicker and in greater abundance than when present in the water column. Collectively these observations suggest horizontal transmission of the symbionts comes primarily from a benthic free-living stage in the sediments (Adams et al., 2009; Coffroth et al., 2006). Under normal, ambient conditions *Symbiodinium* spp. are lost from corals at rates of 0.1–1% per day (Bhagooli and Hidaka, 2004; Hoegh-Guldberg and Smith, 1989; Jones, 1997; Jones and Yellowlees, 1997; Stimson and Kinzie, 1991) and these could be the ultimate source of symbionts for horizontal transmission.

The next stage is the process of budding i.e. formation of daughter, secondary polyps and Hayashibara et al. (1997) reported this occurs in *Acropora secale* after 2 months (Figs. 1 and 3, Table 2) similar to rates reported for *A. millepora* and *A. tenuis* (Graham et al., 2013; Little et al., 2004). Acquisition of algal symbionts and also the type (clade) of symbionts is important for post-settlement survival (Suzuki et al., 2013) bud formation and budding rate (Graham et al., 2013; Little et al., 2004). Gamete-spawning species typically become reproductive at 4–5 years or older (Harrison and Wallace, 1990; Wallace, 1985b) although reproduction is related more to size than age, and for *Acropora* spp., newly formed areas in actively growing regions are typically initially sterile, especially when polyps were budded after the time of onset of gametogenesis (Wallace, 1985b) (Fig. 1).

### 8.1. Effects of sediment on metamorphosis and new recruits

Several studies have measured decreased recruitment rates in the field along quantified eutrophication gradients including spatial (Dikou and van Woesik, 2006; Hunte and Wittenberg, 1992) and temporal gradients (Thompson et al., 2014). Manipulative studies are more common and Sato (1985) conducted one of the first manipulative experiments to examine grazing on post-settlement survival in *P. damicornis*. Larvae were settled in the laboratory on plastic, pre-conditioned petri dishes

and then fixed back on the reef-flat oriented facing upwards, downwards or sideways. Some petri dishes were covered with a 1 cm mesh to protect from grazing. All larvae in the upwards facing dishes (either protected or unprotected) became rapidly smothered in sediment and died, while higher survival was noted in the downward facing petri dishes. Sato (1985) discussed the significance of algae trapping and thereby exacerbating the effects of sediments on larval survival but sediment deposition rates were not quantified.

Babcock and Smith (2002) extended their in situ study with rammed earth bricks and household scrubbing pads (see above) to several months, by episodically adding sediment bricks to ensure a continued sediment supply. After 8 months, the number of settled larvae in the sediment treated sites was only ~40% of the levels in the reference sites suggesting further mortality had occurred from the first census immediately following settlement of the larvae.

Cause–effect pathways associated with the effects of sediment on new recruits are likely to be similar to those of the adult corals and include covering by sediment and loss of autotrophic and heterotrophic feeding and reduced gas/metabolite exchange (metabolite exchange in Fig. 4). The smaller size of recruits however may make them more susceptible to smothering and/or low light stress from elevated sediment concentrations (see Fig. 5C, D, E).

## 9. Conceptual models and cause–effect pathways

Fig. 4 shows the conceptual model of the effects of sediments from dredging on the early life-history stage of corals based on the previous discussion. The framework used to connect the many possible cause–effect pathways and the interrelationship between the stressors is the US Environmental Protection Agency (USEPA) Causal/Diagnosis Decision Information System (CADDIS) (Norton et al., 2009; USEPA, 2004). The process allows the generation of a graphical display, of all known cause–effect linkages, steps along causal pathways and possible interacting stressors. The framework allows the inclusion of biologically plausible but as yet untested cause–effect pathways and, if parameterized, could ultimately form the basis of numerical process model to examine the risks of dredging during coral spawning.

Dredging activities can have both direct and indirect effects on benthic habitats with direct effects including the loss of organisms and habitat by removal of hard and soft substrate within the dredge footprint. Indirect and associated with either (1) sound or (2) ‘turbidity-generation’ or ‘plume creation’ from various dredging methodologies. Sound originates from propellers, pumps, drag and cutting heads, and engine and mechanical noise from dredges and support vessels. There has been much progress in recent years in characterizing of dredging sound and this has mostly been within the context of understanding the effects on marine mammals and fish (WODA, 2013). Sound can ‘mask’ biologically relevant signals and could result in reduced coral settlement success as noted above. A potentially beneficial effect of sound could be avoidance of dredging areas by planktivorous fish which may reduce predation on gametes and larvae. It is too early to evaluate the significance of these mechanisms as compared to the more well-known effects of increased water column suspended sediment concentrations.

The most likely cause–effect pathways associated with the effects of dredging is associated with turbidity-generating i.e. the release of sediment into the water column through a range of different processes (see Foster et al. (2010) and VBKO (2003)). Proximate stressors (or causal agents) can be grouped into physical effects and chemical effects (Fig. 4). Chemical effects are associated with legacy contaminants (pollution) and nutrient release from pore-water or sorption/desorption processes in the water column, and oxygen depletion. Nutrient release has the potential for direct metabolic effects and adverse effects through phytoplankton and microbial blooms and subsequent changes via oxygen concentrations. Contaminants have the potential for acute and chronic toxicological, cellular and physiological effects, including

genotoxic (mutagenic, teratogenic and carcinogenic) effects (Fig. 4), as well as bioaccumulative effects through uptake and ingestion of contaminants (see for example Hedge et al., 2009). Prior to dredging sediments are normally examined for contaminant concentrations and if levels exceed screening guidelines (see for example DEWHA (2009)) are landfilled. Many capital dredging projects in the tropics are also green-field sites without historical pollution, and sediment contamination is a more significant issue for the marine environment of industrialized and typically temperate countries than for tropical benthic coral reef environments (with a few notable exceptions—see Jones (2011)). For these reasons the chemical effects are not considered further here.

The model graphically highlights some of the complexities associated with understanding the effect of sediments on the early life-history stages of corals. While some proximal stressors such as the effects of sound are isolated and distinct, most of the proximate stressors are associated with the release of sediment into the water column and once turbidity has been generated, the proximal stressors then become highly interlinked. Individual stressors become part of a causal pathway to other stressors (the inner triangle of Fig. 4).

This model highlights the multifaceted interactions of sediments with coral reproductive processes and early life history stages. Part of this complexity is due to multiple ways in which corals are affected (e.g. light reduction, physical interactions in the water column and smothering). The model also highlights that dredging and natural resuspension may affect more than one step in the reproductive sequence of corals. When the impacts on each step are documented then this should be accounted for in risk assessment modeling. Although this model reveals multiple stressor pathways, many of which have not been documented previously, it has not considered that other simultaneous stressors such as high sea surface temperature can increase the sensitivity of coral reproduction in an additive or synergistic way (Negri and Hoogenboom, 2011).

## 10. Discussion and conclusions

Turbidity and sedimentation are two of the most widely recognized threats to coral reefs (Johannes, 1970; Risk and Edinger, 2011; Rogers, 1990). There have been many studies of the effects of typically very high SSCs and sedimentation rates on adult corals, but the effects on coral communities may equally manifest themselves over longer periods and associated with changes at the population level via effects on reproduction and recruitment. This review was partly motivated by a recent resources boom in tropical Australia, the need for dredging for coastal infrastructure and shipping channels to export mineral and petroleum products, and current environmental regulations around protecting coral spawning events during dredging campaigns. However, the findings are equally as applicable to natural events in turbid-zone communities driven by wind-wave induced resuspension (Anthony et al., 2004; Jing and Ridd, 1996; Larcombe et al., 1995, 2001; Lawrence et al., 2004; Ogston et al., 2004; Verspecht and Pattiariatchi, 2010).

When the regulations were introduced in Western Australia, shortly after the discovery of co-ordinated spawning of corals comparatively little was known about the effects of sediments, hence the approach was precautionary (Kriebel et al., 2001). Since then an improved understanding of the biology of the early life-history stages of corals and also their response to sediments, coupled with a growing understanding of the water quality conditions that can occur during dredging programs, has allowed a more thorough analysis of the potential risks associated with turbidity generation on the early stages of the coral reproductive cycle.

The conceptual model (Fig. 4) highlights known and also biologically plausible cause–effect pathways including some potentially beneficial effects of turbidity. Benefits include a reduction in UV light penetration potentially reducing damage to gametes and embryos at the surface, a reduction in oxidative stress in symbiotic larvae and recruits (Abrego

et al., 2012; Yakovleva et al., 2009), a reduction in predation rates by reduced visibility and increased encounter rates of aposymbiotic larvae with sediment-associated free-living *Symbiodinium* released into the water column. Suspended and deposited sediments can act as an energy source for adult corals if it contains organic material (Anthony, 1999; Mills et al., 2004), and possibly recently settled corals—although this has yet to be examined. However, there are overwhelmingly more (30+) possible causal pathways whereby turbidity-generating activities can negatively affect reproduction.

Most studies of the effects of sediments have been associated with fertilization and subsequent larval development and settlement, but there is a suite of biologically plausible cause–effect pathways associated with turbidity-generation prior to these stages. The predictability of broadcast spawning corals in some species (to within a few minutes from year-to-year, Vize et al. (2005) and Babcock and Heyward (1986)) and subtle differences when gametes are released by different species, and even factors such as egg–sperm bundle dissociation rates (Wolstenholme, 2004), highlight the significance of timing and the synchronization process for successful fertilization. The time-window for fertilization could perhaps be less than an hour in vivo where sperm dilution and advection occurs (Omori et al., 2001). The available evidence also suggests that it is only very subtle changes in light quantity and quality (i.e. falling light intensities, the length of a period of darkness and the intensity and color of downwelling irradiance during twilight) (Babcock, 1984; Boch et al., 2011; Hunter, 1988; Knowlton et al., 1997; Sweeney et al., 2011) that are amongst the final discrete, proximate triggers for the spawning. This needs to be contrasted with the profound effects of high SSCs on light including producing extended darkness and semi-dark, caliginous, twilight periods. Altering the final cues could result in asynchronous spawning. The extended twilight periods could also affect gametogenic synchrony in the weeks and months leading up to spawning. Such a loss synchrony could ultimately affect the arrival of the gametes at the surface, blurring the temporal separation for each species which is believed to be an important pre-zygotic isolating barrier that prevents or reduces hybridization between closely-related species spawning at slightly different times (Fukami et al., 2003; Knowlton et al., 1997; Levitan et al., 2004; van Oppen et al., 2002; Willis et al., 2006; Wolstenholme, 2004).

A second suite of cause–effect pathways occurring before fertilization include the binding of sediments to egg–sperm bundles reducing ascent rates from the seabed and even cause ascent failure at very high SSCs (Ricardo et al., submitted). Even if not bound to the bundles, settling of silt-sized sediments could affect bundle rise rates, especially for deeper corals, also impacting the timely appearance at the surface. Sedimenting silt-sized particles, which are about the same size as coral sperm, could increase the sinking rates of the already negatively buoyant sperm from the upper-surface where fertilization occurs. As with the effects of light quality and quantity, collectively these mechanisms could also affect the temporal separation resulting in asynchrony and reducing the chances of egg–sperm encounter (Ricardo unpublished data).

Several studies have examined the effects of sediment on fertilization but with wide ranging effects, and it is clear that there is a need for greater standardization of approaches and consideration of experimental conditions such as egg and sperm concentrations and sperm contact times. Attention to these factors may also optimize the sensitivity of the assays for further use in risk models. As a generalization, embryogenesis appears to be relatively less sensitive to the suspended sediment concentration but more studies are needed on the effects on embryogenesis and early larval development to better understand the impacts on the planktonic phase. Early embryos are known to be very sensitive to turbulence, resulting in disintegration of embryos of *A. millepora* at the 2–16 cell stage creating irregular groups of cells or individual blastomeres (Heyward and Negri, 2012). To assess the effects in the water column alternative experimental approaches may be needed to keep the delicate embryos and larvae in suspension together with

uniform sediment concentrations as well as allowing for water exchanges. Future studies will also need to address suitable end-points and how to account for disintegration and disappearance of the larvae which will also deteriorate water quality and affect the remaining larvae (Gilmour, 1999; Nozawa and Okubo, 2011).

The available laboratory and field studies suggests that one of the most sensitive stages is the effects of sediment on settlement and subsequent metamorphosis. High SSCs will affect light quality and quantity reducing the size of potential settlement areas by reducing available light and depth of the photic zone. However, in addition to light related changes, Johannes (1970) specifically linked the effects of sediment on settlement within the context of environmental damage ‘...no new corals can establish themselves where the soft, shifting sediments have covered the once hard calcareous substrate...’. These observations have been substantiated in the exposure conditions has been elusive, except perhaps with the recent work of Perez et al. (2014).

Much like the cascade of environmental variables operating alone or in combination at increasingly finer time scales to co-ordinate reproduction and spawning, Gleason and Hofmann (2011) describe a hierarchy of cues related to settlement, operating at sequentially finer scales and ultimately leading to the choice of a settlement site that is optimal for adult fitness (see also Suzuki et al. (2012)). The presence of sediment seems to be one of the more important final (negative) cues in this cascade, but how sediment is detected by the planulae is unknown. Possible mechanisms include masking of settlement cues and the failure of cnidae to attach in the presence of unconsolidated sediment. The sensing of sediments could occur by receptors on the brim of the concave structure of the aboral pole (Okubo and Motokawa, 2007), and better understanding of the detection mechanism is needed to establish causal relationships.

One of the least studied and potentially most sensitive life-history stages is the early post-metamorphosis survival where the sub-millimeter sized polyps often gain symbionts, start heterotrophic feeding (zooplanktivory) and develop secondary polyps. High post-settlement mortality rates (>90%) are well known in most free-spawning marine invertebrates (Gosselin and Qian, 1997) but the small size of the new recruits makes them difficult to study, and also vulnerable to a range of factors including sediment smothering. This is arguably one of the most important information needs with respect to the effects of sediment from dredging-related and natural turbidity events. Understanding the mechanism whereby sediments can affect the early life-history stages is essential for deriving dose-response relationships and ultimately for providing information that can be useful for management.

The conceptual model (Fig. 4) highlights some of the difficulties associated with establishing dose-response relationships and in particular the conflation of proximal stressors which could potentially confound establishing causal links. While some of the stressors are isolated and distinct, such as effects of sound, other proximal stressors are highly interlinked. Thus, suspended sediments can cause biological effects directly (i.e. by interfering with feeding), but high SSCs are also a step in the causal pathway to another proximal stressor, changes in light quantity (and quality). Similarly elevated SSCs are a necessary precursor to sediment deposition, which by veneering the corals' surface with a fine layer of sediment also reduces light availability and thus the mode-of-action of would also include those associated with light attenuation.

This close interlinking of proximate factors (the inner triangle in Fig. 4) makes it difficult to distinguish which factor or factors are responsible for observed effects in the laboratory or field and to establish quantitative relationships. This needs to be carefully considered in interpreting the results of past laboratory or field manipulations (Table 1) and for designing future studies. For example, Te (1992) found no effects of a 1000 mg L<sup>-1</sup> sediment concentration on settlement of *P. damicornis* planulae in shallow, shaded bowls; however, at that concentration all light would be attenuated in situ within a meter (Te, 1997). Settlement and survival of planulae under those conditions

seems improbable. The pooling of results from past studies, as is common in review articles, can be very misleading unless the wider context of the treatment on other causal pathways is known: only then can the results be used in any kind of environmental context.

The causal/diagnosis decision information system (CADDIS) framework laid out in Fig. 4 has proved useful for identifying areas of uncertainty, knowledge gaps and guiding future laboratory or field studies. If used in combination, with the analysis of the timing of the various life-history stages, and the water quality characteristics during a dredging program over similar time periods, experiments can be designed with more environmentally relevant exposure conditions (Harris et al., 2014). Approximately 200 m from a trailer suction dredge SSCs can exceed hundreds of mg L<sup>-1</sup> for short periods (hours) encompassing the duration of some of the stages in the life-cycle such as the fertilization window. Over longer time frames (i.e. days to weeks), which encompass embryogenesis and the pre-competent and competent stages through to settlement, average SSCs are lower in the tens of mg L<sup>-1</sup> range. Close to a dredge light levels can be reduced to zero for several days to a week. The 95th percentile of the data over the different time frames probably represents close to a worst case scenario but the intensity and duration of the disturbances will decrease with increasing distance from the turbidity-generating activity. While it is clear that water quality conditions (SSCs, sedimentation and light attenuation) during dredging have the potential to harm various early life stages of corals, much work needs to be done to improve experimental stress protocols before the risk to coral reproduction can be assessed. This needs to be considered in interpreting the results of past laboratory or field manipulations (Table 1).

Establishing relationships in situ is difficult because of operational exclusion zones frequently found around dredges and the associated flotilla of hopper barges, bunkering, crew transfer and support vessels. If studies are conducted in the laboratory they will need to overcome the often difficult problems associated with manipulating and keeping sediments in suspension. To derive accurate dose-response relationships for gametes, embryos and larvae it is essential that SSCs are quantified gravimetrically as opposed to being expressed nominally (Harris et al., 2014). Future studies will need to use suitably sized sediment particles, and undertake analyses of particle size distributions. Future studies will also need to undertake a full suite of organic and inorganic chemical analyses as part of normal ecotoxicological procedures (Klimisch et al., 1997) to discount effects of legacy contaminants. These can be significant even in non-industrialized reefal environments. Chemical analyses should be conducted of the typically fine clay and silt fractions used in the assays and not the coarser, bulk surficial sediments from the collection point. The use of clean aragonite or calcium carbonate sediments with similar particle size distributions is recommended as a positive control (Harris et al., 2014; Klimisch et al., 1997) and surrogates for sediments such as carborundum or kaolin clay should not be used. Attention to these details will assist in interpreting the results, verifying the conditions of the assay are optimized and working properly (Harris et al., 2014), and controlling for the effects of contaminants. Future studies need to identify cause-effect pathways, and recognize the effects of treatments on other potential cause-effect pathways and consider the dose-response relationships. Where appropriate statistical metrics such as EC<sub>10</sub> and EC<sub>50</sub> values need to be derived rather than statistical testing of a few point concentrations (Chapman et al., 1996, 2001; Harris et al., 2014; Landis and Chapman, 2011).

The successful use of a coral spawning environmental window as a management tool depends upon a shutdown period which encompasses the entire period that turbidity-generating activities could have an effect on spawning and ultimately the successful recruitment of juveniles into the next generation. The window needs to contain sensitive stages such as settlement and early post-settlement survival (Trapon et al., 2013a; Vermeij and Sandin, 2008). From an operational perspective the success is also reliant upon the bracketing of an easily identifiable, discrete and highly co-ordinated spawning period. In Western

Australia there is a well-known main autumn spawning period (Simpson, 1985), but more recently a significant spring spawning period has been identified (Rosser and Gilmour, 2008). The presently applied 12 days coral spawning shutdown period is too short to fully encompass the full settlement period, and all potential demographic bottlenecks associated with recruitment, especially settlement and early post-settlement survival (see Figs. 2 and 3). Extending the window for a few months before and after the predicted spawning date seems an obvious next step to also accommodate effects on gametogenic and spawning synchrony and to fully cover the settlement period. The window would also need to accommodate both the major (autumn) and minor (spring) spawning period as well split spawning events which occur every 2–3 years. This would significantly limit time that turbidity-generating activities could occur near coral reefs in any given year. Although the approach seems logical, the question is whether this approach is reasonably practicable and whether the resulting intermittent and protracted dredging operation would result in a better net environmental benefit than a shorter campaign. Conducting maintenance dredging activities away from coral spawning periods and settlement periods, and starting capital dredging programs at appropriate times to avoid spawning periods would constitute a best management practice.

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## Author contributions

RJ, GR, and AN wrote the review.

## Competing interests

The authors have declared no competing interests exist.

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