



## Coral reproduction in Western Australia

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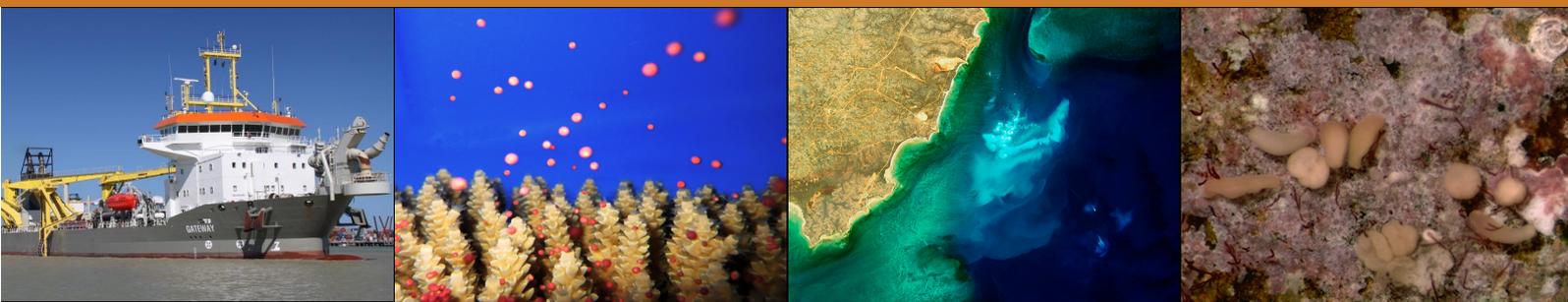
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## WAMSI Dredging Science Node

### 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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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



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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: Spawning of egg-sperm bundles during spring at Scott Reef, Western Australia. (Photo: J Gilmour 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: Coral larvae exploring substrata, attaching and undergoing metamorphosis, following mass spawning in autumn at Ningaloo, Western Australia. (Photo: J Gilmour AIMS)

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## Executive Summary

Larval production and recruitment underpin the maintenance of coral populations, but these early life history stages are vulnerable to extreme variation in physical conditions. Environmental managers aim to minimise human impacts during significant periods of larval production and recruitment on reefs, but doing so requires knowledge of the modes and timing of coral reproduction.

Most corals are hermaphroditic or gonochoric, with a brooding or broadcast spawning mode of reproduction. In brooding corals, sperm are released into the water column but the fertilisation of eggs and the subsequent development of larvae occur within the parent's polyps prior to their release. Brooding corals are a significant component of some reefs and produce larvae over consecutive months.

In broadcast spawning corals, gametes are released into the water column where fertilization and larval development occurs. Broadcast spawning corals are more common, but display considerable variation in the times of spawning and the degree of synchrony among species and colonies on reefs around the world. Reproductive activity in spawning corals is highly seasonal, with peaks in activity often occurring over a few months in many parts of the world. Spawning among species and colonies can be highly synchronised, culminating in the release of gametes during a few nights each year (mass spawning), or may be protracted over many nights and several months. Species of broadcast spawning corals are commonly hermaphroditic, but may also be gonochoric (male or female colonies).

The discovery of mass spawning on Western Australia (WA) reefs occurred at a similar time to that on the Great Barrier Reef (GBR). However, there have since been fewer detailed studies of coral reproduction in WA, due largely to the remoteness of the reefs and the lack of infrastructure to support scientific research. The recent industrial expansion into these regions has facilitated research, but the associated data are often contained within confidential reports. Here we combine information for tens of thousands of corals and hundreds of species, from over a dozen reefs spanning 20 degrees of latitude, based on grey-literature and published reports to comprehensively update our knowledge of coral reproduction in WA.

Most studies investigated spawning in *Acropora* corals over a few months at several reefs, usually within the Kimberley oceanic region, the inshore Pilbara or at Ningaloo, leaving large spatial and temporal gaps in knowledge. Nevertheless, patterns of spawning seasonality and synchrony are evident from across the vast expanse of WA's coral reefs. There is a gradient in the spawning activity of most corals among seasons, with mass spawning during autumn occurring on all reefs (apart from the temperate southwest).

Participation in a multi-specific spawning during spring decreased from roughly 25% of corals on the Kimberley oceanic reefs to little or no multi-specific spawning in spring at Ningaloo, where spawning may be more protracted.

Within these seasons, mass spawning occurred most commonly in March and/or April, and the multi-specific spawning in October and/or November, or can be split over the two consecutive months depending on the timing of the full moon. Split-spawning typically occurs every few years, but can also occur in consecutive years, and will dramatically affect inferences about the participation by colonies and species in spawning events if only one of the two months is sampled.

On most WA reefs, there is still a poor understanding of monthly variation in spawning and comparatively few data available for non-*Acropora* corals, which may have different patterns of reproduction. For example, the massive *Porites* appear to spawn through spring to autumn on Kimberley oceanic reefs and in summer in the Pilbara region. Other common corals such as *Turbinaria* and *Pavona* also displayed different patterns of reproduction to the *Acropora*. Brooding corals (*Isopora*, *Seriatopora*) on Kimberley Oceanic reefs appeared to release larvae during many months, possibly with peaks from spring to autumn and a similar pattern is likely on other WA reefs. Gaps in knowledge were also due to the difficulty in identifying species and methodological issues.

This review provides a brief summary of the methods and sampling protocol for quantifying patterns of reproduction in corals and an approach to quantifying the relative significance of periods of reproductive output that may occur throughout the year. Hypothetical examples are provided, and the approach provides a basis for further development of a method to quantify the importance of reproductive periods for maintaining coral communities, which is useful for managing dredging and construction operations around coral spawning seasons.

## Considerations for predicting and managing the impacts of dredging

Critical windows of environmental sensitivity, such as the predictable mass spawning of corals, are often considerations in the environmental impact assessment of infrastructure projects in the tropical northwest (see EPA 2016<sup>1</sup>). When the timing of construction overlaps with mass spawning events, proponents are often required to manage turbidity generating activities to reduce pressure during these periods as a condition of approval. The principle behind such requirements is that if coral reproduction, settlement and recruitment are concentrated during a discrete period, then the potential for impacts on corals can be reduced by suspending turbidity generating activities such as dredging and spoil disposal around mass spawning events. Although coral mass spawning is reasonably predictable, it varies between species and locations, and so it is important to ensure any stoppages coincide with the spawning event for it to be effective. Furthermore, cessation of dredging can be costly and can delay the completion of projects. Therefore, studies of coral reproduction are vital in predicting the appropriate window in which dredging or construction should be suspended to reduce impacts and to satisfy Ministerial Conditions attached to the approval of such activities whilst not un-necessarily restricting construction activities.

Most studies infer mass spawning on WA reefs occurs at night based on the presence of pigmented eggs in colonies, with very few direct field observations of spawning and limited sampling conducted after the event. Based on the few studies that have directly observed the nights of mass spawning on tropical WA reefs, it is assumed more widely to occur with a peak seven to nine nights after the full moon, within a predicted month. However, mass spawning during some years can occur several days outside of the predicted period and has been observed as early as three days after the full moon, while more intensive sampling at some reefs has documented other exceptions to this general rule. **Although our knowledge of coral reproduction throughout WA is incomplete, a general pattern is evident that can largely be attributed to variation in 1) community composition, 2) latitude and 3) the timing of the full moon.**

### Community Composition

The most obvious differences in reproductive patterns to arise from community composition is due to the abundance of brooding versus spawning corals. Some of the most common brooding coral on WA reefs include the *Isopora*, *Seriatopora* and *Stylophora*. Gametogenesis and planulation (larval release) probably occur over several months within the year, most likely around the full moon during most months through spring to autumn.

Within the spawning assemblages, differences in the times of spawning are often due to the varying abundances of *Acropora* and some non-*Acropora* species. For example, spawning times on offshore and tropical WA reefs vary according to the abundance of Acroporidae and massive *Porites* colonies, and on inshore reefs spawning times vary according to the abundances of Faviidae, Pocilloporidae, *Turbinaria* and/or *Pavona*.

### Latitude

Latitudinal variation in gametogenesis and planulation in brooding corals on WA reefs is unknown. Brooding corals are likely to have multiple gametogenic cycles on all WA reefs, although the number of cycles within the population versus within individual colonies is unknown.

In contrast, there is a clear pattern of latitudinal variation in spawning corals. Within a year, most individuals have a single cycle of gametogenesis that culminates in spawning during one or a few consecutive nights

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<sup>1</sup> EPA 2016 *Technical Guidance: Environmental Impact Assessment of Marine Dredging Proposals*. EPA, Western Australia.

each year. **The primary period of spawning on all WA reefs (apart from the southwest region) is in autumn, often culminating in the mass spawning of a relatively high proportion of species and colonies during March and/or April.** Successive studies have added to the list of species known to mass spawn during autumn, but also to the list known to participate in a second multi-specific spawning during spring (October and/or November) on some northern WA reefs. The existing data suggest that biannual spawning by communities during autumn and spring is a phenomenon that occurs at lower latitudes, with increasing frequency from Ningaloo Reef north. In addition to this reduced participation in a spring spawning, the autumn spawning may also become more protracted over consecutive nights with increasing latitude.

### **The timing of the full moon and neap tides**

Within the main seasons of spawning, temporal variation in spawning times is not well understood, particularly for the multi-specific spawning in spring.

Available data indicates that autumn spawning will be split between March and April (and possibly February) in almost all years, with the majority of spawning occurring seven to nine nights after the full moon within a given month coinciding with the neap, nocturnal, ebb tides. March is normally the month with the highest spawning activity however in some years, spawning may be more evenly split between March and April or may occur predominantly in April.

Whether spawning occurs predominantly during the first (e.g. March) or second (e.g. April) month of the season, or is split over the two months, depends on the timing of the full moon. This is due to differences in the length of solar and synodic months (1 synodic month = 1 lunar month = 29.53 days). As a result the timing of lunar phases occurs 10-12 days earlier in each calendar year and for reproductive seasonality to be maintained over time, spawning must be delayed at some stage (about every 3 years).

As a general rule in the Pilbara, spawning that is predicted to occur between 8-24 March in any year, is considered likely to result in a major spawning in March, with smaller contributions in February and April. If spawning is predicted to occur between 1 and 7 March, spawning is likely to be split between March and April, with one month having a greater participation rate than the other. If spawning is predicted to occur between 25 and 31 March, then spawning is likely to be split between February and March with one month having a greater participation rate.

On oceanic reefs, a full moon in late February and early March generally results in a mass spawn in March or a split-spawning in March and April; a full moon in mid to late March may lead to a mass spawn in late March or early April.

In addition, rates of gametogenesis are strongly influenced by water temperatures. There is anecdotal evidence that with increasing ocean temperatures spawning may be occurring earlier; some colonies may be spawning in February and/or a higher proportion in March during hot years. However, many years' data are required to validate such a shift in reproductive patterns. In contrast, the full moon has an obvious effect on the time of spawning. Because of these sources of uncertainty field sampling is always recommended in order to confirm the month of major spawning.

The effect of the timing of the full moon on the spring spawning period has been far less studied and is less understood.

### **Pre-development Surveys**

Many early studies of coral reproduction employed a rigorous sampling design and complimentary methods because so few data existed. From these studies, it is clear that quantifying community reproductive output during a given period is far easier if prior data exist for the dominant taxa through different seasons and years. For example, these background data inform whether: common taxa are likely to brood planula several times per year, participate in mass spawning events once or twice a year, or to spawn at other times of the year; histology or *in situ* sampling should be applied; the timing of the full moon may result in an early, late, or split-spawning. **Prior to designing a sampling regime, the literature specific to reefs within the different regions of WA should**

be read thoroughly, as with the primary literature that provides background to the application of different methodologies and the patterns of reproduction for corals more widely.

#### *Quantify Community Composition*

Pre-development surveys of coral reproduction would benefit from first quantifying the community composition. Doing so allows the methods and sampling design for reproductive assessments to be driven by the relative cover of different coral groups, and data on abundance and reproduction can be combined to quantify the significance of periods of reproductive output within a year. For environmental management, information regarding coral reproduction is often required at the level of the entire community. As the taxonomic list for tropical coral reefs can be extensive, a convenient cut-off point can be chosen according to their cumulative contribution to total coral cover (e.g. 80%); consideration must also be given to whether certain species, although low in relative abundance, play a critical role in ecosystem function.

#### *Choose appropriate taxonomic unit for classification*

The choice of taxonomic units for quantifying community composition and reproductive patterns on a reef also requires considerable thought. The identification of many coral species on tropical reefs is extremely difficult, particularly from photographs and *in situ*. **Although identification to the finest taxonomic resolution is always desirable, it may only be practical for species that are particularly abundant and are easily identifiable from photographs and *in situ*. For other species, it is more important to ensure identifications at higher taxonomic levels are correct.** Depending on the diversity of species and the taxonomic skills of the researchers, a practical approach to quantifying composition and reproduction in coral communities may be to group species according to a higher taxonomic level (e.g. Genus, Family) and to also consider growth form (e.g. massive, branching, encrusting) and reproductive mode (spawner, brooder). The advantage is that uncertainty around the identity of species is obvious, rather than records of incorrectly identified species becoming entrenched in the literature. Such approaches are valid where the objective of management is to protect reef integrity by ensuring resilience of the coral assemblage at a functional level.

### **Monitoring**

#### *Sampling design*

Once the community composition of the reef has been quantified and the background data on reproduction for dominant corals explored, the sampling methods and design can be resolved. **In most instances, a single sample prior to a predicted date of spawning is insufficient to quantify reproduction during a given period.** The exception is perhaps if only a short period of impact is being considered and sufficient background data exist to ensure the sampling approach is rigorous. In most instances, a single annual sample is a weak basis for inference, particularly when spawning is split or staggered, for species that have protracted spawning seasons, or for brooding corals. **Without comprehensive data, surveys from previous years provide few insights into future spawning events, requiring substantial sampling effort to be repeated prior to every period of interest. In the worst instances, focusing only on the participation by species in a single month risks perpetuating a paradigm of mass spawning or missing a significant period of reproductive output.**

Dominant corals should be sampled throughout the potential reproductive seasons to determine the relative magnitude of reproductive output in the year. A key factor in the logical process of determining whether or not spawning has taken place is the construction of a series of data points that demonstrates the development of gametes and their subsequent disappearance after spawning. In this case, reliance on random sampling alone is insufficient for those corals that do not spawn entirely in a single month. Oogoneic cycles in spawning corals take several months, so in species known to spawn biannually (March and October) or over a protracted period (September to April) eggs will be present in the population during most months. There is no evidence of corals spawning during winter months, so detailed sampling in this period is not necessary. A sampling program to determine the proportion of species and colonies spawning or releasing planulae throughout the year should, however, span several months from the start of spring to the end of autumn.

### *Sampling methodology*

**The presence of mature testes, eggs (pigmented) or larvae (in brooding species), followed by their subsequent disappearance, is the best basis for making strong inferences about the timing of spawning. The optimal time of sampling will depend on the assemblage.** If using testis development and/or egg pigmentation to infer participation in a spawning event, particularly in communities dominated by *Acropora*, it is useful to sample approximately one week before the predicted night; more than a week and eggs may not yet be pigmented, while less than a week the chances of missing an early spawning increases. It is important to note that in many corals, particularly the Acroporidae, eggs may not be pigmented more than two weeks prior to spawning and that unpigmented eggs may also be spawned, highlighting the need for large sample sizes and for sampling to be conducted following spawning events. In other taxa, particularly some Faviidae, pigmented eggs may not be pink or red (e.g. green), and pigmentation may occur two months or more before spawning. It is also vital to know whether species of interest are hermaphroditic or gonochoric, as the absence of eggs in visual surveys of male colonies may be incorrectly interpreted as a low participation in a spawning event.

In addition to re-sampling the assemblage through time, tagged colonies ideally should be resampled if there is doubt about whether the absence of gametes is due to a spawning event, or due to variation in the timing of spawning among colonies within a population. Using tagged colonies to supplement a random sample of the population through time can be particularly useful for populations that spawn during two or more discrete periods in the year (e.g. March and April, or autumn and spring). Consideration must obviously be given to the number of samples that can be taken from a single colony, so as not to cause significant stress and divert energy investment away from reproduction.

### *Sample size*

**Sample sizes must be adequate to account for the background variation in reproduction among species within the community, among conspecific colonies during a year, and among years.** If all colonies are spawning during the same month, then the level of replication required is small – but considerable sampling is first required to establish this trend and it is uncommon for many species on most reefs. Relying on a fixed sample size for all species can become problematic when colonies spawn during different months, different seasons, if stressed colonies are not reproducing, if they have separate sexes, or if spawning during a year is split. The required replication can range from a few colonies per species when all spawn synchronously over a few nights each year, to many more colonies for assemblages with mixed patterns of reproduction during some years. It is important to note that the absence of eggs in a colony provides few insights into broader patterns of reproduction, further highlighting the need for sufficient replication. Additionally, not all polyps within a colony may be reproductive, so multiple samples from single colonies are advisable. **We argue that for most WA reefs it is better to first sample the most abundant species rigorously (in the context of overall community composition) to determine their pattern of reproduction, rather than sample most species within low replication.**

**A detailed understanding of the methods used to quantify reproduction in corals and their advantages and limitations is required.** Methods used to quantify reproductive patterns for coral communities include: direct observations of spawning, larval recruitment to artificial substrata, *in situ* examination of eggs, microscopic examination of eggs and testes, histological examination of eggs and testes. **The choice of methods will depend on the community composition and information required, but the most informative studies involve sequential sampling of colonies using a combination of complementary methods.** For example, determining the times of spawning in hermaphroditic species may involve monthly examination of eggs in preserved samples. As eggs approach a size in which spawning is likely, then preserved samples may be supplemented or replaced by *in situ* and microscopic examination of the sizes and developmental stage of eggs and testes. When the night of spawning is predicted within a given month, then *in situ* and microscopic examinations of eggs and sperm are continued on a daily basis around the predicted nights of spawning, possibly supplemented by *in situ* observations of spawning and evidence of spawn slicks the following day. For gonochoric species, colonies can

be tagged and their sex determined using histology. Female colonies may then be tagged and resampled to track the developmental stages of eggs, while the night of spawning can be determined with *in situ* and microscopic investigation of eggs and testes in colonies of both sexes. Similarly, for brooding corals histological examination may establish the months of gametogenesis and planulation, while *in situ* and microscopic examination can inform the weeks or even nights of spawning. On all reefs, a proportion of species and colonies typically spawn over several nights, so continued sampling is required to quantify the proportion of colonies without eggs and to identify the main night of mass spawning within a period.

Since the discovery of mass coral spawning, the phenomenon has been documented on an increasing number of reefs around the world. In many of these studies, sampling has been conducted around the main periods of spawning on the nearest reefs and focused on species of *Acropora*, which are most likely to spawn synchronously and are easiest to sample. However, fewer studies have provided detailed information about cycles of gametogenesis in spawning corals and planulation in brooding corals during other months of the year, despite some common species not participating in the primary spawning event(s) on a reef. For example, on inshore reefs of WA's Pilbara region *Acropora* may be relatively rare, whereas species of massive *Porites*, *Turbinaria* and *Pavona* that have more extended and only partially overlapping spawning periods of reproduction may be among the most common. Even on reefs where the *Acropora* are among the most common genera (25% by cover), such as on the oceanic reefs of the Kimberley, other common groups of corals such as the massive *Porites* (20%), *Isopora* (14%) and Pocilloporidae (10%) also have different reproductive modes or cycles.

#### *Determining significance of spawning periods*

**An accurate assessment of the significance of periods of reproductive output requires knowledge of the proportion of colonies within each species releasing gametes or larvae during many months of the year. Additionally, several years of data with varying environmental conditions are required to understand the drivers of inter-annual variation, such as whether a low participation in a spawning event was due to environmental stress or split-spawning. A lack of accurate and unbiased information about times of reproductive output by coral communities impedes management initiatives aimed at reducing pressures to their early life history stages.** Managers would ideally be provided with quantitative estimates of the reproductive output during different weeks, and even nights of the year, and its contribution to the long-term maintenance of populations. Obtaining this knowledge is currently impossible, but it is possible to obtain estimates of reproductive output in different months of the year by combining the relative abundance of coral groups with the proportion spawning or releasing larvae. Careful consideration must first be given to the assemblage of corals that best characterises the reef coral community based on percentage cover data. A decision must then be made about whether all taxa are to be included, or whether sampling effort can be reduced by excluding rare corals. This significantly reduces effort, as finding and sampling rare species with sufficient replication is most time consuming. Care must obviously be taken in deciding the threshold for including dominant species in a 'community' and the means by which they are categorised (see comments above in relation to taxonomic units).

**Once the relative estimates of abundance and reproductive timing are obtained for common taxonomic groups, the data can be combined to produce estimates of reproductive output by the community throughout the year.** This is one of several possible approaches to quantifying temporal variation in reproductive output for an entire community throughout the year, to aid management decisions. The approach is intended to identify the months in which significant reproductive output occurs at the scale of the entire community, and more detailed temporal sampling within these months is required to determine the nights of spawning and planula release relative to the phases of the moon. In the context of managing environmental impacts, there may be other factors to be considered, beyond the approach based on relative abundance. For example, important species like massive *Porites* may not be dominant in terms of cover but can be functionally important species because of their contribution to reef three-dimensional structure. The proportion of reproductive output each month will vary among years according to changes in community structure and particularly the occurrence of split-spawning or environmental stress. Consequently, several years of data collection are required to obtain a reasonable understanding of reproduction on the reef before sampling effort can be reduced. **It is recommended that a data base be established that can be built over time to improve understanding of different reefs and**

regions of WA. Any such data base should have good quality assurance procedures in place to allow appropriate inferences to be made (see below).

## Residual Knowledge Gaps

### Background literature and the application of methods

**Gaps in current knowledge have resulted from errors in sampling. A good knowledge of the primary literature on coral reproduction, and the advantages and disadvantages of different methods is required before studies are designed and executed.** In the simplest cases, insufficient meta-data associated with samples make it impossible to inform regional patterns of reproduction, such as whether samples were collected from inshore or offshore reefs in a region, or the exact date of collection relative to the timing of the full moon. In other instances, participation in a seasonal spawning event was uncertain because only one month of a split-spawning was sampled, or because the presence of pigmented eggs was used as an indicator more than a few weeks before the predicted spawning (when eggs are not yet pigmented) or in species known to be gonochoric (in male colonies). Harder to address is the profound difficulty in identifying many tropical coral species *in situ* and the resulting variation spawning times for individual species, or the resulting variation in the estimated proportion of colonies and species participating in a spawning event (often used to define ‘mass spawning’). For these reasons, a considered approach to species identification is required, and uncertainty should be acknowledged by grouping similar species or applying a higher taxonomic unit, in conjunction with using definitions of mass spawning based on the proportional cover of coral taxa in the relevant coral assemblage. Other such errors in sampling methods or design have led to inappropriate conclusions, which in turn confuse generalisations about patterns of reproduction in the reef and apparent gaps in knowledge.

### Biases in species and methods

Most studies of coral reproduction in WA have been conducted over a few months at several reefs. As with many other reefs around the world, initial sampling employed visual surveys of egg pigmentation within *Acropora* corals prior to a predicted mass spawning. As studies on WA reefs increased and diversified in approach, the variation in reproduction among reefs, with latitude and community structure, become more evident. Although far more balanced, our current understanding of coral reproduction on WA reefs is still biased by a disproportionate amount of data for spawning *Acropora* from a few reefs and times. **For many coral species on WA reefs, modes of reproduction, sexuality, cycles of gametogenesis, and the time of maturation for eggs (pigmentation) and sperm prior to spawning are largely unknown. Additionally, reproductive information for coral species is constantly being revised.** The assumed reproductive mode (brooder, spawner) and sexuality (gonochoric, hermaphroditic) for a species can change with further research, and varies among reefs around the world. Even among WA reefs this can vary from that previously assumed for some species (e.g. *Pocilloprora*), while other species are commonly assumed to have the same pattern of reproduction as similar taxa. **When sampling targets the *Acropora* or species are incorrectly assumed to be hermaphroditic mass spawners, the estimated participation in a single mass spawning will be biased because of the few data describing alternate patterns of reproduction.** On WA reefs, research in the Dampier Archipelago best illustrates the issue, where detailed investigations have found that common species of massive *Porites*, *Turbinaria* and *Pavona* are not hermaphroditic mass spawners. More widely, little is known of the patterns of reproduction of other common species (e.g. Faviidae, *Porites*, *Montipora*) that make important contributions to the structure of many WA reefs. **If species are common on a reef, it is important that their mode or reproduction and sexuality are known before sampling methods and design are streamlined.**

### Latitudinal patterns

**Economic development projects in WA has facilitated many studies of coral reproduction, so the amount of available data often reflects the requirements set out by regulators. However, gaps in knowledge among reefs across WA also reflect their accessibility and the complexity of the reproductive patterns.**

On the **Kimberley oceanic reefs**, there is a good understanding of the participation by corals in the biannual spawning events, but this also is biased towards the *Acropora* and there are few data for other times of the year. For the **inshore reefs of the Kimberley**, there are very few reproductive data. Many corals probably participate in the same biannual spawning events as the oceanic reefs, but whether the spawning periods are more protracted around those two events or through the summer months is unknown.

The patterns of reproduction in **Pilbara reefs** are probably the most complex of all regions in WA. Several studies have been conducted within the Dampier Archipelago, providing valuable insights into the regional patterns, but few data are available for the wider Pilbara region. Within the region, reefs transition between the times of spawning in the Kimberley and Ningaloo. Communities in the Pilbara spawn predominantly during autumn, but there is also some participation in a spring spawning; periods of reproduction through these seasons may be more protracted than on the northern reefs and species common to the Pilbara display distinct cycles of reproduction.

On **Ningaloo Reef**, spawning occurs predominantly during autumn, and there is only anecdotal evidence of spawning during spring. However, spawning during autumn may be more protracted over a greater number of nights, weeks, and months, with evidence of spawning in some species during summer. Whether or not these more protracted periods of reproduction are unique to Ningaloo, or simply reflect the finer temporal sampling, remains to be determined.

At the **Abrolhos Islands**, many corals are known to participate in mass spawning during autumn, with no evidence of multi-specific spawning during spring. However, a relatively high proportion of colonies and some species did not contain gametes at the time of sampling, suggesting they spawn at other times of the year or are potentially gonochoric or brooding corals.

There are few available data for the temperate reefs at **Rottneest Island and in the southwest of WA**, which seem to have most unique patterns of reproduction. They are the only reefs not to have a high proportion of species and colonies mass spawning over a few nights during autumn, although spawning is evident over a protracted period through summer to autumn.

### **Seasons, months, weeks, nights and times of spawning**

There is a reasonable understanding of seasonal variation in spawning times for WA reefs, and ways in which the timing of the full moon can affect the months of spawning. However, most studies have focused on the predicted month(s) of mass spawning with methods sufficient to infer the week of spawning. The degree of synchronous spawning by corals over one or two nights within a year varies among WA reefs. **But the extent to which spawning is protracted over days to weeks, around the main night(s) of spawning, or weeks to months around the main month of spawning, is unknown for most reefs.** Although far from conclusive, existing data suggests that spawning is most synchronous over a few consecutive nights during autumn and then spring on oceanic reefs, and perhaps in the northern Kimberley, and becomes more protracted over several nights or weeks around a single autumn spawning on southern reefs at Ningaloo and the Abrolhos Islands. A region of transition between synchronous biannual spawning on northern reefs and a more protracted single spawning on southern reefs seems to be evident in the Pilbara. **For brooding corals, the exact timing of the release of sperm for internal fertilisation of eggs and the subsequent release and settlement of developed larvae is also unknown for all reefs.** Regulators often require industrial activities to shut-down for a period of approximately one week around a single night(s) of predicted mass spawning. **Without a knowledge of the proportion of species and colonies releasing gametes on a predicted night of mass spawning, then the proportion of gametes, larvae and new recruits that are protected from turbidity generating activities during a shut-down period cannot be estimated.**

# Coral reproduction in Western Australia

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## ABSTRACT

Larval production and recruitment underpin the maintenance of coral populations, but these early life history stages are vulnerable to extreme variation in physical conditions. Environmental managers aim to minimise human impacts during significant periods of larval production and recruitment on reefs, but doing so requires knowledge of the modes and timing of coral reproduction. Most corals are hermaphroditic or gonochoric, with a brooding or broadcast spawning mode of reproduction. Brooding corals are a significant component of some reefs and produce larvae over consecutive months. Broadcast spawning corals are more common and display considerable variation in their patterns of spawning among reefs. Highly synchronous spawning can occur on reefs around Australia, particularly on the Great Barrier Reef. On Australia's remote north-west coast there have been fewer studies of coral reproduction. The recent industrial expansion into these regions has facilitated research, but the associated data are often contained within confidential reports. Here we combine information in this grey-literature with that available publicly to update our knowledge of coral reproduction in WA, for tens of thousands of corals and hundreds of species from over a dozen reefs spanning 20° of latitude. We identified broad patterns in coral reproduction, but more detailed insights were hindered by biased sampling; most studies focused on species of *Acropora* sampled over a few months at several reefs. Within the existing data, there was a latitudinal gradient in spawning activity among seasons, with mass spawning during autumn occurring on all reefs (but the temperate south-west). Participation in a smaller, multi-specific spawning during spring decreased from approximately one quarter of corals on the Kimberley Oceanic reefs to little participation at Ningaloo. Within these seasons, spawning was concentrated in March and/or April, and October and/or November, depending on the timing of the full moon. The timing of the full moon determined whether spawning was split over two months, which was common on tropical reefs. There were few data available for non-*Acropora* corals, which may have different patterns of reproduction. For example, the massive *Porites* seemed to spawn through spring to autumn on Kimberley Oceanic reefs and during summer in the Pilbara region, where other common corals (e.g. *Turbinaria* & *Pavona*) also displayed different patterns of reproduction to the *Acropora*. The brooding corals (*Isopora* & *Seriatopora*) on Kimberley Oceanic reefs appeared to planulate during many months, possibly with peaks from spring to autumn; a similar pattern is likely on other WA reefs. Gaps in knowledge were also due to the difficulty in identifying species and issues with

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methodology. We briefly discuss some of these issues and suggest an approach to quantifying variation in reproductive output throughout a year.

**Subjects** Marine Biology, Science Policy

**Keywords** Coral reproduction, Spawning corals, Brooding corals, Coral reefs, Western Australia, Coral larvae, Coral recruitment

## INTRODUCTION

### Reproduction in scleractinian corals

Sexual recruitment underpins the maintenance of most coral communities, so knowing their peak times of reproductive output is critical to the management of human activities that reduce recruitment to the adult population. Larval production, recruitment, and early post-recruitment survival in corals are reduced by extreme variation in physical factors such as temperature and salinity (*Bassim, Sammarco & Snell, 2000; Harrison & Wallace, 1990; Harrison, 2011; Negri, Marshall & Heyward, 2007*) or degraded water quality (*Gilmour, 1999; Harrison & Ward, 2001; Humphrey et al., 2008; Markey et al., 2007; Negri & Heyward, 2001*). Model projections highlight the implications of prolonged reductions in larval recruitment for the maintenance of coral populations, and particularly their recovery following disturbances (*Babcock, 1991; Done, 1987; Edmunds, 2005; Fong & Glynn, 2000; Gilmour et al., 2006; Smith et al., 2005*). The times of reproduction also influence the community recovery via connectivity to other coral reefs (*Gilmour, Smith & Brinkman, 2009; Done, Gilmour & Fisher, 2015*). For example, the larvae of brooding corals are released several times a year under a range of hydrodynamic conditions, but typically disperse over relatively short distances (< several kilometres), whereas the larvae of spawning corals are produced during one or a few discrete periods, and disperse over larger distances (> several kilometres). A detailed understanding of community reproduction is therefore required to mitigate human activities around critical periods of larval production and to inform the design of management networks reliant on estimates of larval exchange (*Carson et al., 2010; Kool, Moilanen & Trembl, 2013*).

Most scleractinian corals have one of four patterns of sexual reproduction, depending on their sexuality (hermaphroditic or gonochoric) and developmental mode (brooding or broadcast spawning) (*Baird, Guest & Willis, 2009; Fadlallah, 1983; Harrison & Wallace, 1990; Harrison, 2011; Richmond & Hunter, 1990*). In brooding corals, the fertilisation of eggs and subsequent development of larvae occur within the parental polyps. Larvae are competent to settle shortly after their release from the polyp, with planulation typically occurring over several months each year. In contrast, colonies of broadcast spawning corals typically release their gametes into the water column once a year, where fertilization and larval development occur, after which larvae disperse for days to weeks before settling. Some coral species (or cryptic sub-species) have more complex patterns of reproduction (e.g. *Pocillopora damicornis*), while blurred species boundaries and flexible breeding systems continue to confound our understanding of reproduction in many coral taxa (*van Oppen et al., 2002; Veron, 2011; Willis, 1990; Willis et al., 2006*).

Reproductive activity in spawning corals can be remarkably synchronised, culminating in the release of gametes by a high proportion of species and colonies during a few nights each year (mass spawning), or spawning by a similar proportion of colonies and species may be protracted over many nights and several months (*Baird, Guest & Willis, 2009; Harrison & Wallace, 1990; Harrison, 2011*). The ultimate factor driving high synchrony, particularly within species, is probably successful fertilisation and larval recruitment. However, a wide range of environmental factors underlie this success and cue spawning over increasingly fine temporal scales, such as water temperature, day length, moon phases and tidal amplitude (*Baird, Guest & Willis, 2009; Guest et al., 2005a; Harrison & Wallace, 1990; Penland et al., 2004; van Woesik, 2010*). These cues all interact to synchronise spawning within communities, so it is tempting to view mass spawning as a phenomenon that occurs at the community level, whereas each species is in fact responding independently to its environment. As conditions vary, gametogenic cycles in each species will respond differently, as their environmental optima may differ or because the environment provides fewer synchronising cues (*Oliver et al., 1988*). Indeed, environmental stress will reduce the energy available for gametogenesis and the likelihood of corals reproducing during a given year (*Michalek-Wagner & Willis, 2001; Ward, Harrison & Hoegh-Guldberg, 2000*), also confounding generalities about spawning patterns. The species composition of reefs changes as environmental conditions vary, further influencing the patterns of reproduction at the reef scale. Clearly there is significant scope for reproduction of coral assemblages on reefs to vary regionally and depart from the ‘mass spawning’ discovered on the Great Barrier Reef (*Babcock et al., 1986; Harrison et al., 1984*) and subsequently pursued by some investigations of coral reproduction around the world. This variation in timing and synchrony results in a range of reproductive patterns, from temporal isolation of spawning species to a highly synchronous mass-spawning.

Mass spawning in scleractinian corals was first discovered on parts of the GBR in austral spring (*Harrison et al., 1984; Willis et al., 1985*), where it is perhaps more synchronous than on any other coral reef worldwide. However, even on the GBR there is a spatial and temporal variation in mass-spawning. For example, the near-shore reefs spawn one month earlier than those on mid- and outer-shelf reefs (*Willis et al., 1985*), while the high- and low-latitude reefs have a more protracted period of spawning at times other than during spring (*Baird, Guest & Willis, 2009; Baird, Marshall & Wolstenholme, 2002; Harrison, 2008; Oliver et al., 1988; Wilson & Harrison, 2003*). Additionally, spawning times within coral assemblages also vary among years according to the timing of the full moon within the spawning window. The date of the full moon occurs several days earlier each month than in the previous year, causing spawning times to shift periodically (e.g. from October–November) if gametes are not yet mature at the time of full moon. Similarly, when the full moon falls near the edge of the spawning window then only some colonies will have mature gametes, so spawning occurs following two consecutive full moons (e.g. October and November). This phenomenon has been termed ‘split spawning’ and typically occurs every few years, but can occasionally occur over consecutive years (*Baird, Guest & Willis, 2009; Willis, 1985*).

Many of the early studies leading to the discovery of mass spawning on the GBR involved rigorous sampling of colonies using a range of methods throughout the year, which established synchronous reproductive cycles within and among populations (Wallace, 1985). This led to more intensive sampling over weeks and days, which established the remarkable synchrony among many colonies and species over a few nights each year. In contrast, some subsequent studies have focused on identifying the species participating in mass spawning events but not quantifying the proportion of participating colonies or the frequency of spawning during other times (nights, weeks, months, and seasons) of the year. Without estimates of the reproductive state of colonies during other times of the year, a relative assessment of the participation in mass spawning events is not possible; if there is a low participation in the mass spawning then there is no knowledge of the other time(s) of spawning, whereas if there is a moderate to high participation then it may be assumed incorrectly that spawning during the other time(s) is negligible. For example, a rigorous sampling of the reproductive state of coral populations throughout the year has identified a second spawning by populations and even some colonies on the GBR (Stobart, Babcock & Willis, 1992; Wolstenholme, 2004) and other reefs around the world (Dai, Fan & Yu, 2000; Guest et al., 2005b; Mangubhai, 2009; Mangubhai & Harrison, 2006; Oliver et al., 1988). Focussing only on the participation of corals in the mass spawning can also miss the times of reproduction for entire species that are common and functionally important, such as the massive *Porites* (Harriott, 1983a; Kojis & Quinn, 1982). Additionally, brooding corals are a significant component of many reefs, and planulation in populations and colonies is typically spread over several months throughout the year (Ayre & Resing, 1986; Harriott, 1992; Harrison & Wallace, 1990; Harrison, 2011; Tanner, 1996).

Despite considerable research effort on the GBR, there is still not a detailed understanding of spatial and temporal variation in coral reproduction at the scale of entire assemblages. This highlights the difficulty in obtaining a similar understanding for the remote coral reefs on Australia's west coast, where far less research has been conducted. Most studies of coral reproduction in Western Australia (WA) have been conducted over a few months at several reefs, of which there are few published accounts (but see Table S1), leaving large gaps in knowledge. The gaps are significant because the existing data illustrate the unique patterns of reproduction displayed by WA coral communities and the extent to which they vary among habitats and regions. The rapid industrial expansion through regions of WA in the last decade has seen an increase in the number of studies of coral reproduction, but much of the associated data are contained within confidential reports to industry and government. Here we combine some of the information in this grey-literature with that in public reports and papers, to update our current knowledge of coral reproduction in WA. This includes data for tens of thousands of corals and hundreds of species, from over a dozen reefs spanning 20° of latitude. From these data we identify broad latitudinal patterns, but many gaps in knowledge remain due to paucity of data, biased sampling, and in some instances poor application of methodology. We therefore conclude with a brief discussion around issues of sampling design and methodology, and suggest one approach to quantifying the

significance of periods of reproductive output by coral communities, which is among the suite of information required by managers to moderate the effects of human activities along Australia's west coast.

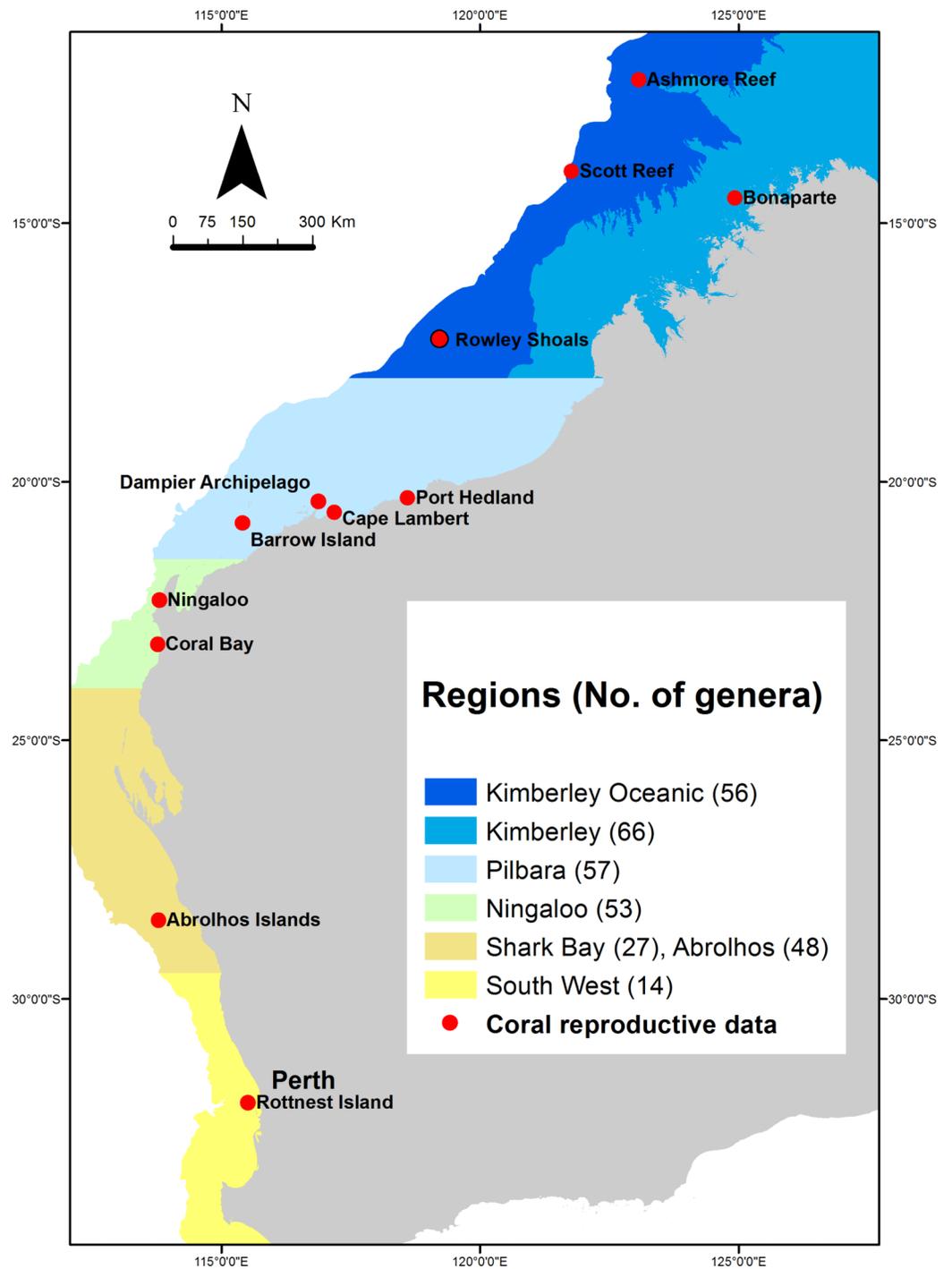
## METHODS

### Western Australian regions and sources of reproductive data

Western Australia's coral reefs span more than 12,000 km of coastline and 20° of latitude, ranging from tropical to temperate climates, from coastal reefs to oceanic atolls hundreds of kilometres from the mainland (*Veron & Marsh, 1988; Wilson, 2013*). Consequently, WA has a phenomenal diversity of habitats and coral communities, with a corresponding range in reef-level patterns of coral reproduction. Because of these broad patterns in coral community composition, the examination of patterns of reproduction presented here is divided among six regions: (1) Kimberley Oceanic, (2) Kimberley, (3) Pilbara, (4) Ningaloo, (5) Abrolhos and Shark Bay, and (6) Rottnest and southwest WA (*Fig. 1*). Among these regions, the diversity of coral species and genera decreases with increasing latitude (*Fig. 1*), although coral cover can be similar among the tropical reefs and those at the subtropical Abrolhos Islands, before then decreasing in the temperate southwest (*Abdo et al., 2012; Johannes et al., 1983; McKinney, 2009; Richards & Rosser, 2012; Richards, Sampey & Marsh, 2014; Speed et al., 2013; Veron & Marsh, 1988*).

Regional data or data summaries of coral reproduction were taken from journal articles and public reports, unpublished data, and confidential reports to industry and government (*Table S1*). Where possible, raw data were interrogated and summaries produced across reefs for each region. However, in other instances raw data were not available and regional summaries were based on tables and text within reports that had not been peer-reviewed. Given the scope of these data, discrepancies also existed among studies and there are likely errors in data collection, analyses and species identification. Some regional summaries were adjusted to account for obvious errors in data or conclusions in some reports and the most likely patterns of reproduction were sometimes extrapolated from limited data. Additionally, samples were typically biased by factors such as the environmental conditions, the community composition, the sampling design and the methods used. For example, inferences about the patterns of reproduction on a reef were heavily biased when: data exist for a few species of *Acropora* but the community was dominated by non-*Acropora* corals that reproduce at different times; environmental stress inhibited gametogenesis causing a large portion of the assemblage not to reproduce in a period; spawning was split over two consecutive months but only one month was sampled; coral species and/or genera were incorrectly identified. The issues were most acute in studies with limited spatial and temporal replication. For these reasons, a summary of information that commonly biases inferences about patterns of coral reproduction is presented for each region, to place in context the reproductive data, and times of spawning for species were assigned a level of confidence according to the available data (*Tables 1, 2 and S2*).

Coral reef habitats of WA are characterised by widely contrasting environments, but all are exposed to considerable wave energy generated by seasonal cyclones and/or storms.



**Figure 1** Regions in which the composition of coral reefs and the proposed patterns of coral reproduction differ most significantly across Western Australia. Numbers in brackets indicate the number of coral genera identified in each region (see Table 1). Red circles indicate reefs at which data on coral reproduction were available, from which inferences about the differences among regions were drawn.

**Table 1 Regional variation in coral diversity and reproduction across Western Australia.** The number of species within each coral genus known to occur within each region of WA, and the number for which reproductive data are available. The percentage of species within each genus known to reproduce in spring or autumn within each region, of the total sampled. Regions are colour coded according to Fig. 1.

Region	Genus	Total known species	Number of species sampled		Spawning % (number) of species sampled	
			Spring	Autumn	Spring	Autumn
Kimberley Oceanic	<i>Acropora</i>	63	39	49	90 (35)	94 (46)
	<i>Echinophyllia</i>	3	1	2	0 (0)	100 (2)
	<i>Favia</i>	13	4	6	75 (3)	100 (6)
	<i>Favites</i>	8	3	3	33 (1)	100 (3)
	<i>Goniastrea</i>	6	2	6	100 (2)	100 (6)
	<i>Hydnophora</i>	4	2	1	50 (1)	100 (1)
	<i>Lobophyllia</i>	3	1	0	100 (1)	–
	<i>Merulina</i>	2	2	2	0 (0)	100 (2)
	<i>Montipora</i>	28	0	0	–	–
	<i>Platygyra</i>	6	0	3	–	100 (3)
Kimberley	<i>Acropora</i>	39	35	16	42 (15)	87 (14)
	<i>Echinophyllia</i>	3	0	0	–	–
	<i>Favia</i>	9	2	1	0 (0)	100 (1)
	<i>Favites</i>	6	2	1	0 (0)	100 (1)
	<i>Goniastrea</i>	7	4	1	0 (0)	100 (1)
	<i>Hydnophora</i>	4	4	0	75 (3)	–
	<i>Lobophyllia</i>	2	2	0	0 (0)	–
	<i>Merulina</i>	1	1	0	0 (0)	–
	<i>Montipora</i>	23	0	0	–	–
	<i>Platygyra</i>	5	3	1	0 (0)	100 (1)
Pilbara	<i>Acropora</i>	49	35	43	34 (12)	98 (42)
	<i>Echinophyllia</i>	2	0	0	–	–
	<i>Favia</i>	10	1	8	0 (0)	87 (7)
	<i>Favites</i>	7	2	4	50 (1)	100 (4)
	<i>Goniastrea</i>	7	5	7	0 (0)	100 (7)
	<i>Hydnophora</i>	4	1	1	0 (0)	100 (1)
	<i>Lobophyllia</i>	3	1	2	0 (0)	100 (2)
	<i>Merulina</i>	2	1	1	0 (0)	100 (1)
	<i>Montipora</i>	28	4	3	0 (0)	66 (2)
	<i>Platygyra</i>	6	4	6	0 (0)	100 (6)
Ningaloo	<i>Acropora</i>	39	17	26	12(2)	92 (24)
	<i>Echinophyllia</i>	2	2	2	0 (0)	100 (2)
	<i>Favia</i>	8	0	2	–	100 (2)
	<i>Favites</i>	8	0	1	–	100 (1)
	<i>Goniastrea</i>	7	1	1	0 (0)	100 (1)
	<i>Hydnophora</i>	4	1	1	0 (0)	100 (1)
	<i>Lobophyllia</i>	4	1	1	0 (0)	100 (1)
	<i>Merulina</i>	2	2	2	0 (0)	100 (2)
	<i>Montipora</i>	28	2	2	0 (0)	100 (2)
	<i>Platygyra</i>	6	1	2	0 (0)	100 (2)

(Continued)

Table 1 (continued).

Region	Genus	Total known species	Number of species sampled		Spawning % (number) of species sampled	
			Spring	Autumn	Spring	Autumn
Abrolhos	<i>Acropora</i>	39	0	20	–	100 (20)
	<i>Echinophyllia</i>	2	0	1	–	100 (1)
	<i>Favia</i>	8	0	5	–	100 (5)
	<i>Favites</i>	8	0	5	–	100 (5)
	<i>Goniastrea</i>	7	0	2	–	0 (0)
	<i>Hydnophora</i>	2	0	0	–	–
	<i>Lobophyllia</i>	3	0	1	–	100 (1)
	<i>Merulina</i>	1	0	1	–	100 (1)
	<i>Montipora</i>	26	0	4	–	100 (4)
	<i>Platygyra</i>	2	0	1	–	100 (1)
South West	<i>Acropora</i>	1	0	1	–	100(1)
	<i>Echinophyllia</i>	0	0	0	–	–
	<i>Favia</i>	1	0	0	–	–
	<i>Favites</i>	4	0	0	–	–
	<i>Goniastrea</i>	3	0	2	–	50 (1)
	<i>Hydnophora</i>	0	0	0	–	–
	<i>Lobophyllia</i>	0	0	0	–	–
	<i>Merulina</i>	0	0	0	–	–
	<i>Montipora</i>	1	0	1	–	100 (1)
<i>Platygyra</i>	0	0	0	–	–	

**Note:**

Dashes lines indicate no data for that genus. Diversity data are summarised from several key references (*Berry, 1993; Berry & Marsh, 1986; Done et al., 1994; Richards et al., 2015; Richards & Rosser, 2012; Richards et al., 2009; Richards, Sampey & Marsh, 2014; Veron, 1993; Veron & Marsh, 1988*).

Reef habitats range from open ocean atolls surrounded by deep oligotrophic waters in the Kimberley Oceanic Region, to reefs heavily influenced by coastal processes such as tidally driven sediment resuspension in the inshore Kimberley and Pilbara Regions. From the coastal fringing reefs of Ningaloo, to the subtropical and temperate reefs at the Abrolhos Island and the Southwest Region, tidal processes are less extreme, waters are clearer and often lower in nutrients. This is due in part to the southward flowing Leeuwin Current which intensifies in winter, moderating winter temperature minima and assisting the transport of coral larvae to southern reefs (*Cresswell, 1996; D'Adamo et al., 2009; Hatcher, 1991*). Consequently, there is a high level of reef development in the sub-tropical reefs at the Abrolhos Islands. While the low latitude reefs in the Kimberley have the highest species diversity, they also experience the most pronounced differences in environmental conditions and community composition between the oceanic reefs and those adjacent to the mainland (*Richards et al., 2015; Richards, Sampey & Marsh, 2014*). Similarly, within the Pilbara Region, community composition differs between the most frequently studied inshore reefs in the Dampier Archipelago where most reproductive data exist, and mid-shelf around Barrow and Montebello islands (*Richards & Rosser, 2012; Richards, Sampey & Marsh, 2014*). More information about the environmental

**Table 2 Regional variation in spawning for coral species sampled most rigorously on Western Australian reefs. Regions are colour coded according to Fig. 1.**

Species	Kimberley oceanic			Kimberley			Pilbara			Ningaloo			Abrolhos			South West		
	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut
<i>Acropora aspera</i>																		
<i>Acropora cytherea</i>																		
<i>Acropora digitifera</i>																		
<i>Acropora florida</i>																		
<i>Acropora gemmifera</i>																		
<i>Acropora humilis</i>																		
<i>Acropora hyacinthus</i>																		
<i>Acropora intermedia</i>																		
<i>Acropora latistella</i>																		
<i>Acropora microphthalma</i>																		
<i>Acropora millepora</i>																		
<i>Acropora samoensis</i>																		
<i>Acropora secale</i>																		
<i>Acropora spicifera</i>																		
<i>Acropora tenuis</i>																		
<i>Favia pallida</i>																		
<i>Favia stelligera</i>																		
<i>Favites halicora</i>																		
<i>Goniastrea aspera</i>																		
<i>Goniastrea australensis</i>																		
<i>Goniastrea retiformis</i>																		
<i>Lobophyllia hemprichii</i>																		
<i>Merulina ampliata</i>																		
<i>Platygyra daedalea</i>																		

**Notes:**

Seasons and months are: Spring, Spr; September, s; October, o; November, n; Summer, Sum; December, d; January, j; February, f; Autumn, Aut; March, m; April, a; May, m. Spawning has not been recorded during Winter months (June, July, August) in Western Australia and they have been excluded. Taxonomic revisions are summarised in Table S2. Based on the available data, the sampling design and the methods used, confidence in the inferred months of spawning were ranked qualitatively according to:

- Confident. Evidence based on the presence of pigmented eggs in colonies prior to the predicted dates of spawning in many colonies, sites and years; the presence and absence of pigmented eggs in many colonies around the predicted dates of spawning; and/or direct observations of spawning in multiple colonies.
- Likely. Evidence based on the presence of pigmented eggs in many colonies prior to the predicted dates but with limited spatial and temporal replication; and/or most evidence indicates spawning during this month but with some contradictory data among studies.
- Possible. Evidence based on the presence of large but unpigmented eggs several weeks prior to the predicted dates of spawning; and/or contradictory data among studies due to sampling design, methodology, or species identification.
- Unlikely. No evidence of spawning; pigmented or large unpigmented eggs absent from samples of many colonies, sites and years within several weeks of the predicted dates of spawning.

characteristics and the context for reef development and coral reproduction in each region is provided in [Supplemental Information 1](#). Preceding the reproductive summary for reefs within each region is information to place these data in context, which includes: the species diversity and community composition of corals; the number and types of reefs, sites and species for which reproductive data were collected and the time(s) of sampling; whether colonies were affected by disturbances at the times of sampling; and the methods used to infer the times of spawning or planulae release.

## RESULTS

### Regional patterns of coral reproduction: Kimberley Oceanic

The oceanic reefs of the Kimberley are atolls rising from depths of several hundred meters, with over 300 species and 57 genera of hard corals. Coral cover in many habitats can be over 70%, and much of the remaining substrata are covered in coralline and turf algae, with a very low cover of macroalgae and other benthic organisms. The Acroporidae are typically the dominant family of hard corals, followed by the Poritidae, Faviidae and Pocilloporidae, while soft corals are also common.

Coral reproduction has been investigated at all of the Kimberley oceanic reefs during one or more years ([Table S1](#)). From Ashmore, Cartier, Scott and Seringapatam Reefs, and the Rowley Shoals, several thousand colonies from over 130 species and 30 genera have been sampled during the autumn and/or spring spawning seasons, in one or more years. Of the total number of *Acropora* species known in the region, approximately 62% were sampled in spring and 78% in autumn, compared to 20 and 32% of non-*Acropora* species, respectively ([Table 1](#)). The majority of the sampling has been conducted at Scott Reef, where there was sampling of colonies prior to the spawning in autumn and spring in consecutive years from 2007–2010, including repeated sampling of some tagged colonies. There has been comparatively little sampling at other times of year, so inferences about spawning during summer months may be underestimated. In most instances, the times of spawning were inferred from in situ ranking of gamete development, in addition to microscopic investigation of egg sizes and histological analyses of some spawning corals and brooding corals. Spawning has also been observed in situ on several occasions.

The existing data suggest that most species of corals on the oceanic atolls are broadcast spawners. Spawning has been inferred to occur primarily during spring and autumn, with a larger proportion of species and colonies participating in the autumn mass spawning than in the multi-specific spawning during spring ([Tables 2](#) and [S2](#)). Many species participated in both spawning events, but most colonies spawn only once a year (i.e. within-population biannual spawning). Of the species of *Acropora* sampled in spring ( $n = 39$ ) and autumn ( $n = 49$ ), 90% were reproductively active in spring and 94% in autumn, compared to 10% in spring and 32% in autumn for the common non-*Acropora* species ( $n = 73$ ) ([Tables 2](#) and [S2](#)). For the species sampled repeatedly over several years, approximately 40% spawned only in autumn, less than 10% only in spring, and approximately 55% in both autumn and spring; within species, a similar proportion (> 30%) of colonies spawning during each season. A similar pattern was evident in the

additional 30 species of *Acropora* and 20 species of non-*Acropora* sampled less rigorously ( $n = 5\text{--}10$  colonies  $\text{yr}^{-1}$ ), but for a higher proportion of non-*Acropora* species and colonies spawning in autumn; *Favia stelligera* and *F. pallida* spawned during both seasons and *Diploastrea heliophora* spawned only during spring (Table S2). More intensive sampling of the non-*Acropora* species may increase the proportion of instances of within-species biannual spawning among these species.

Within each season, spawning most commonly occurred during March and October, but varied according to the timing of the full moon. Split-spawning occurred every few years during both seasons and occasionally over consecutive years; splits usually occurring between March and April in autumn, and October and November in spring, following full moons that fell in the last week or so of the preceding months. Spawning has been observed directly in autumn and/or spring during six years, and colonies were sampled before and after to check for the disappearance of pigmented eggs. Based on these observations, spawning usually occurred 7–9 nights after the full moon during neap tides. However, the times of spawning varied among years and occurred any time from the night of the full moon to around 10 days after.

The majority of corals showed evidence of spawning either in March and/or April, and October and/or November, with the exception of the massive *Porites*. At the times of sampling during autumn and spring, pigmented eggs were observed in only a few massive *Porites* colonies, but massive *Porites* can spawn eggs with comparatively little pigmentation (Stoddart, Stoddart & Blakeway, 2012). Histological analyses of samples collected at these times indicated that colonies were dioecious and released eggs and sperm over several months in the year from spring to autumn. A peak in reproductive activity was not obvious, and stages of gamete development indicated spawning over several months from October–May, in contrast to the peak in spawning observed in massive *Porites* on other reefs around Australia (Kojis & Quinn, 1982; Stoddart, Stoddart & Blakeway, 2012). The sampling of all species was restricted a few months each year around two main spawning events, and the extent of spawning following other lunar phases and months has not been investigated in detail. The potential exists for at least some colonies and/or species to spawn during other times. For example, a small proportion of *Acropora millepora*, *A. tenuis*, *A. polystoma*, *A. gemmifera* and *Goniastrea edwardsii* colonies at Ashmore Reef had pigmented eggs in early February or September 2011, indicating they would either spawn a month earlier than most other corals or would retain their eggs until the next month; alternately, early spawning in some corals during 2011 could reflect higher than normal water temperatures. In addition the variation in times of broadcast spawning, larval production in the brooding corals also occurs outside of the dominant spawning events. Histological analyses confirmed that *Isopora brueggemanni*, *I. palifera*, *Seriatopora hystrix* and *Stylophora pistillata* were brooding corals in the offshore Kimberley region. *Isopora brueggemanni* and *S. hystrix* were most intensively sampled and contained gametes in all stages of development and planula larvae during most months from October–May. There was no clear peak in reproductive activity in the brooding corals and larvae were apparently released over many months from spring to autumn.

## Regional patterns of coral reproduction: Kimberley

There are diverse and extensive reef systems throughout Kimberley region, including inner shelf, fringing and patch reefs, exposed platforms and subtidal banks around the coastline and islands (Richards, Sampey & Marsh, 2014; Speed et al., 2013; Wilson, 2013). There are over 300 species of hard corals from 71 genera, and clear cross-shelf differences in species distributions exist between the coastal and offshore locations, with 27 species (8%) recorded only from nearshore locations and 111 species (33%) recorded only at offshore locations (Richards, Sampey & Marsh, 2014). There are no quantitative data describing the relative abundances of corals throughout the inshore Kimberley, but qualitative descriptions highlight the considerable variation in habitats and coral assemblages. For example, leeward intertidal reefs may be characterised by branching and tabular *Acropora*; subtidal zones can have a high cover and diversity of corals dominated by massive *Porites* and species of Faviidae and foliose corals; exposed fringing reefs may have a comparatively low cover and diversity of corals dominated by massive Faviidae and soft corals; extensive tidal pools throughout the region can have a high cover and diversity of corals different to those in other zones (INPEX, 2011; Wilson, 2013).

There are very few reproductive data for coral assemblages in the inshore Kimberley region, particularly given the extent and diversity of the reefs (Table S1). Inferences of coral reproduction in the region are largely based on surveys during one or two years at a small group of islands within the Bonaparte Archipelago (Fig. 1). Several hundred colonies from around 60 species and 15 genera were sampled during autumn or spring season, with sampling focusing on species of *Acropora* (Tables 1 and S2). Of the total number of *Acropora* species known in the region, approximately 90% were sampled in spring and 40% in autumn, compared to 30 and 4% of non-*Acropora* species, respectively. Inferences about spawning during these seasons were drawn from in situ or microscopic examination of pigmented eggs within colonies, and there are no observations of coral spawning for the inshore Kimberley reefs.

The main season of spawning on inshore Kimberley reefs is probably during autumn, but with second multi-specific spawning also occurring during spring at a similar time to the oceanic reefs in the region (Tables 2 and S2). Of the species of *Acropora* sampled in spring ( $n = 35$ ) and autumn ( $n = 16$ ), 42% were inferred to spawn in spring and 87% in autumn (Table 2). Of the 60 common non-*Acropora* species, there was evidence of only 5% spawning in spring and 7% in autumn. The low proportion of non-*Acropora* spawning at these times suggests reproductive activity outside the peak spring and autumn spawning windows by these taxa, and/or is a consequence of low replication and a possible split-spawning. Although not observed in situ, spawning by a few species of Mussidae and Faviidae in aquaria at Kimberley Marine Research Station (KMRS) at Cygnet Bay occurred at a similar time as at the oceanic reefs during two years, 7–9 nights after full moon in March (A. McCarthy & A. Heyward, 2012, personal communication). There is currently no evidence of spawning in the inshore reefs of the Kimberley occurring a month earlier than on the oceanic reefs, as tends to occur on

parts of the Great Barrier Reef. If this was to occur in the Kimberley, spawning on the inshore reefs would be expected in February or March in autumn, and September or October in spring. Although sampling has not been conducted during these months, the existing data demonstrate that spawning did not occur exclusively a month earlier than on the oceanic reefs and that multi-specific spawning events have also occurred later in the season, during April in autumn and November in spring. Evidence for late spawning during autumn and spring may reflect a split-spawning during the years of sampling, as on the oceanic reefs.

Of 31 species sampled from seven genera on the inshore Kimberley reefs during late March, 30 had pigmented eggs and were likely to spawn in early April. This included many species that were sampled with low ( $\leq 5$  colonies) replication, indicating that autumn is the main season of spawning. Indeed, based on the timing of the full moon and spawning on the oceanic reefs, the autumn spawning during that year (2007) was likely spilt; so many colonies and species may have also spawned in early March, providing further evidence for autumn being the primary season of spawning for the region. Of 63 species sampled in late October, 25% contained pigmented eggs and were likely to spawn in early November, of which the majority were *Acropora*; 37% of the 35 species of *Acropora* contained pigmented eggs. However, eggs were absent from many of the colonies sampled with low replication ( $\leq 5$  colonies) and the spring spawning may have been split, based on the timing of the full moon and the data for the oceanic reefs. Consequently, a proportion of colonies and species probably spawned in early October and future work may identify a higher proportion of species and colonies participating in a spring spawning. It remains to be determined whether the inshore reefs of the Kimberley display a similar degree of spawning synchrony during any one month in autumn and spring as on the oceanic reefs, or whether inshore spawning is more protracted over several months with seasonal peaks around autumn and spring, as may be the case on Indonesian reefs to the north ([Baird, Guest & Willis, 2009](#)). There are few data for the non-*Acropora* corals, which are most likely to have less synchronous patterns of spawning, and nor are there currently any data for brooding corals that are probably common throughout parts of the region. The brooding corals in the Kimberley are likely to display similar patterns of reproduction to those at the oceanic reefs, with planulation occurring during many months through spring to autumn, and perhaps extending into some winter months.

### Regional patterns of coral reproduction: Pilbara

There are extensive near-shore and mid-shore reefs systems throughout the Pilbara. Within the region much of the available information exists for the Dampier Archipelago (e.g. [Blakeway & Radford, 2004](#); [Griffith, 2004](#); [Marsh, 2000](#); [Richards & Rosser, 2012](#); [Veron & Marsh, 1988](#)) and there is less information for reefs in the west Pilbara (but see [Marsh, 2000](#); [Richards & Rosser, 2012](#); [Veron & Marsh, 1988](#)). The general pattern of coral diversity is similar throughout the Pilbara, with between 200 and 230 species recorded at the Dampier Archipelago, and at the mid-shore Montebello and Barrow

Island reefs. A slightly higher number recorded at the Dampier Archipelago may be due to greater diversity of habitats and environmental conditions (Griffith, 2004; Marsh, 2000; Richards & Rosser, 2012). However, there are distinct assemblages of coral species among the inshore reefs and those throughout the archipelago, reflecting the cross-shelf variation in environmental conditions and habitat types (Blakeway & Radford, 2004; Richards & Rosser, 2012). Average total hard coral cover for the inshore reefs of the Pilbara is approximately 20%, with the dominant families Faviidae and Dendrophylliidae having contributed to much of this cover (Speed et al., 2013). However, coral community composition can also vary dramatically among the inshore reefs and species of *Acropora*, Faviidae, *Platygyra*, *Turbinaria* and *Pavona* are common in some communities (Blakeway & Radford, 2004). The outer reefs of the west Pilbara can have communities characteristic of clearer water, with approximately twice the coral cover and a higher diversity. In particular, within the back-reef habitats many massive *Porites* colonies are associated with extensive coral assemblages, including a high cover (> 50%) of *Acropora* (Marsh, 2000; Speed et al., 2013).

Coral reproduction in the Pilbara region has been investigated at several reefs, with over 1,000 colonies sampled from 115 species, during one or more years (Table S1). Of the total number of *Acropora* species known in the region, 71 and 88% were sampled in spring and autumn, respectively, compared to 28 and 46% for the non-*Acropora* species (Tables 1 and S2). By far the majority of these data were from the Dampier Archipelago, and the times of reproduction were inferred from in situ ranking of gamete development, microscopic investigation of egg sizes and histological analyses of some spawning and brooding corals. Spawning has also been observed in situ on several occasions. Given the frequency and timing of disturbances to Pilbara reefs in recent years, including dredging operations, temperature anomalies and cyclones, some data from the region were probably biased by coral colonies having insufficient energy reserves to invest in reproduction. In these instances, the proportion of species and colonies reproducing could be underestimated.

The first discovery of coral spawning in Western Australia was in the Dampier Archipelago (Simpson, 1985). Early research showed corals spawning exclusively in autumn over two consecutive years, in 46 species of coral from seven families. The presence of mature eggs in some non-*Acropora* species after the main spawning event indicated split-spawning over two consecutive lunar cycles, but there was no evidence of spawning during spring. Subsequent research has documented multi-specific spawning by a small proportion of colonies and species during spring (October–December). Within the Dampier Archipelago, a small number of tagged colonies seemed to spawn consistently either in autumn or in spring and have only one gametogenic cycle. Of the species of *Acropora* sampled in spring ( $n = 35$ ) and autumn ( $n = 43$ ), 34% were inferred to spawn in spring and 98% in autumn (Tables 2 and S2). Of the 69 common non-*Acropora* species, 43% spawned in autumn and one spawned in spring, although few were sampled in spring. Among the non-*Acropora* species, only *Favites flexuosa*, and possibly *Favites pentagona* and *Montipora undata* are thought to spawn in spring or early summer, while the proportion of colonies within species of *Acropora* known to spawn

during spring is generally low (< 20%) (Tables 2 and S2). Sampling around a split-spawning and with environmental stress has potentially underestimated the participation by corals in the spring spawning (October–December), but the primary spawning period is certainly autumn (usually March).

Many Pilbara reefs are dominated by corals such as massive *Porites*, *Pavona decussata* and *Turbinaria mesenterina*, which display different patterns of reproduction to most hermaphroditic species that participate exclusively in the spring and/or autumn spawning events. Within the Dampier Archipelago, repeated histological examination showed that these three taxa were gonochoric. Spawning occurred predominantly in December in the massive *Porites* (mainly *P. lobata*), as on the Great Barrier Reef (Harriott, 1983a; Harriott, 1983b). For *Pavona decussata*, spawning occurred during March and April, possibly due to split-spawning during that year (2007). In *Turbinaria mesenterina*, spawning occurred over several months, possibly from November–April. While *T. mesenterina* retained eggs after this period, this does not indicate imminent spawning as this species has been reported to have a gametogenic cycle of more than 12 months (Willis, 1987). While spawning has not been observed, frequent sampling of *P. lutea* demonstrated that it spawned during spring tides predominantly 3 days (2–4 days) after the full moon, in contrast to the usual times of spawning during neap tides approximately one week after the full moon. In addition to these spawning corals, the main periods of reproductive output for the brooding corals in the Pilbara are also likely to occur at times other than during the dominant spawning periods in autumn and spring. Although cycles of gametogenesis in brooding corals have not yet been investigated in the Pilbara, they probably culminate in the release of planula larvae over several months through spring to autumn, and possibly into winter months.

### Regional patterns of coral reproduction: Ningaloo

Ningaloo is an extensive fringing reef system almost 300 km in length, with diverse coral communities and over 200 species of hard corals from 54 genera (Veron & Marsh, 1988). Mean coral cover can be as high as 70% at areas of the reef flat and reef slope, but is typically less at other habitats such as in the lagoon (Speed et al., 2013). The remaining benthic cover is composed of coralline and turf algae, seasonal macroalgae growth and other benthic organisms. Within the coral communities, the Acroporidae are often most abundant, but the Faviidae, Poritidae, Pocilloporidae and soft corals are also common (Speed et al., 2013; Veron & Marsh, 1988). The deeper lagoons typically contain massive *Porites* bommies and patches of staghorn *Acropora*, while the outer-slope is dominated by robust corals with massive and encrusting growth forms, often *Platygyra sinensis* and prostrate *Acropora* (Wilson, 2013).

There is detailed reproductive data for some species at one location at Ningaloo and a comparatively poor understanding of spatial variation across this extensive system (Table S1). Coral reproduction has been investigated during several years, for several hundred colonies from 42 species and 11 genera (Table 1). Of the total number of *Acropora* species known in the region, approximately 44% were sampled in spring and 67% in autumn, compared to 14 and 20% of non-*Acropora* species, respectively.

Most data exist for several species of Acroporidae and Faviidae sampled during one or more months from spring to autumn at Coral Bay. Early work at Ningaloo suggests some variation in the time of spawning may exist among locations, with a higher proportion of corals spawning in March in the north and in April to the south, but this may also have been a consequence of split-spawning. Nonetheless, the studies of coral spawning at Coral Bay provide detailed information about temporal variation in spawning among months, lunar cycles, and the nights of spawning in autumn. Inferences about spawning times were drawn from in situ ranks of gamete development and microscopic investigation of egg sizes in random population samples and by re-sampling individual colonies, in addition to direct observations of spawning in situ.

Mass spawning at Ningaloo occurs during autumn, with a more protracted period of spawning over consecutive months, and little or no multi-specific spawning during spring (Tables 2 and S2). Of the species of *Acropora* sampled in spring ( $n = 17$ ) and autumn ( $n = 26$ ), 12% were inferred to spawn in spring and 92% in autumn, with one spawning exclusively in summer. Of the 69 common non-*Acropora* species, none were reproductively active in spring, compared to 20% in autumn (Tables 2 and S2). However, a low proportion of species ( $< 20\%$ ) and particularly colonies have been sampled during spring. Additionally, there are very few reproductive data from parts of Ningaloo other than Coral Bay. Most Acroporidae and Faviidae colonies at Coral Bay participated in mass spawning during a single month in autumn, but a small proportion of many species also spawned during other months through summer and autumn. Species typically spawned during one or two consecutive months, with no evidence of spawning during discrete months or of a multi-specific spawning during spring, as on northern reefs. There are numerous observations of slicks of coral spawn during spring, but the extent to which these are a product of multi-specific spawning remains unknown (R. Babcock & D. Thompson, 2015, personal communication). Within species, individual colonies had a single gametogenic cycle and usually spawned within a few consecutive nights. The mass spawning usually occurred during neap tides in late March or early April, 7–10 nights after the preceding full moon, but a small proportion of colonies of several species also spawned following the full moon or the new moon during months either side of the mass spawning.

Within the species spawning during autumn, most of their colonies (60–100%) participated in the mass spawning in early April following the full moon in late March, but during other years mass spawning occurred in the last week of March following an earlier full moon in March. Around the quantified mass spawning events in early April, a relatively small ( $< 20\%$ ) proportion of colonies from most species also spawned a month earlier (early March) or later (early May), following the preceding full moon or new moon, particularly in the non-*Acropora* species. A higher proportion (10–20%) of these colonies spawned during March than in May ( $< 10\%$ ), which may be due to a split-spawning during the years of sampling or may be typical of a more protracted spawning at Ningaloo. Early observations suggest that split-spawning is a common feature at Ningaloo, but whether it occurs during the same years and involves a similar proportion of species and colonies as on reefs further north remains to be determined.

Cooler waters at Ningaloo could result in slower rates of gametogenesis and an increased likelihood of split-spawning during years in which a full moon falls early in March, and/or a higher proportion of colonies participating in an April spawning than on northern reefs.

There was little evidence of spawning at Ningaloo during months other than in autumn. Less than a few percent of colonies of *Goniastrea retiformis*, *A. humilis* and *A. papillarae* had visible eggs in October, but none were pigmented and the times of spawning were unknown. Existing data suggests that *A. papillarae* is the only species that does not participate in mass spawning and spawns exclusively during summer, probably during December and/or January. Additionally, a small proportion (< 5%) of *Echinopora lamellosa* also spawned during summer in February, but with a higher proportion spawning during March ( $\approx 13\%$ ) and particularly April ( $\approx 80\%$ ). There are currently no data for species of corals such as massive *Porites* known to spawn during summer at other reefs throughout WA. Given that spawning seems to be more protracted at Ningaloo, future work may identify a higher proportion of species and colonies spawning during summer, particularly for the non-*Acropora*. There is also no existing information for the times of planulation in brooding corals at Ningaloo, but planula release is likely to occur at similar times to other northern reefs, from spring through to autumn, with perhaps a lower incidence in spring due to the cooler water temperatures.

### Regional patterns of coral reproduction: Abrolhos Islands and Shark Bay

The Houtman Abrolhos Islands have the highest latitude coral reefs in Western Australia. The coral communities are scattered among four islands, situated < 100 km from the coastline but near the edge of the continental shelf, with over 180 species from 42 genera of corals (*Veron & Marsh, 1988*). Coral cover ranges between 35 and 85% among habitats (*Dinsdale & Smith, 2004*), with an average cover for the region of approximately 44% (*Speed et al., 2013*). Unlike studies on a comparable latitude on the east coast of Australia (*Harriott & Banks, 2002*), the Abrolhos maintains high percentages of tabulate and particularly staghorn *Acropora* (*Abdo et al., 2012; Dinsdale & Smith, 2004*). Much of the remaining substrata were covered in turf and coralline algae, although patches of macroalgae are also common. Situated to the north of the Abrolhos Islands, Shark Bay is a large shallow bay ( $\sim 12,950 \text{ km}^2$ ) with an average depth of 9 m and is enclosed by a number of islands (*Veron & Marsh, 1988*). The bay consists of vast seagrass meadows (*Wells, Rose & Lang, 1985*) and coral growth is restricted to waters with oceanic salinity, such as in the western side of the bay (*Veron & Marsh, 1988*), where 82 species from 28 genera of hard corals have been recorded (*Veron & Marsh, 1988*). Corals from the families Acroporidae and Dendrophylliidae are found in similar abundance of approximately 10–15% cover, and other genera found in low (< 2%) cover include *Montipora*, *Platygyra*, *Pocillopora*, and *Porites* (*Bancroft, 2009; Cary, 1997; Moore, Bancroft & Holley, 2011; Speed et al., 2013*).

Coral reproduction has primarily been investigated during 1 year at the Abrolhos Islands, around the predicted time of mass spawning in autumn (*Table S1*). Of the total

number of species known in the region, approximately 49% of the *Acropora* and 34% of the non-*Acropora* were sampled in autumn, but with no sampling at other times of the year (Table 1). Several hundred colonies from 107 species and 10 families were sampled in March 1987, and a small random sample of colonies during late February 2004 (Table S2). Most samples were from species of *Acropora* and Faviidae around the Wallabi group of islands. The times of spawning were inferred from in situ ranking of gamete development, microscopic investigation of egg sizes and stages, and direct observation of spawning in situ and in aquaria. In addition to random sampling, tagged colonies were re-sampled before and after the main nights of spawning.

There is clearly a mass spawning by a high proportion of many *Acropora* species at the Abrolhos Islands during autumn, but no knowledge of whether corals also spawn during spring or summer (Tables 2 and S2). Of the 107 species sampled, 58 species participated in the main two nights of spawning in March, with a further 36 species likely to spawn on other nights during March; a similar proportion of *Acropora* (49%) and non-*Acropora* (31%) participated in the March spawning. Spawning occurred primarily over the 10 and 11 nights after the full moon, during spring tides of small amplitude (< 2 m), with reports of other spawning events also between 8 and 11 nights after the full moon. In addition to the species and colonies that spawned over a few consecutive nights, there was also evidence of a more protracted spawning by many colonies and species over a greater number of nights, and possibly also during April and/or other seasons. Within the species of mass-spawners, the mean number of colonies participating was 70%, and ranged between 10 and 100%. Most species spawned over a few nights, but within the assemblage spawning was probably protracted over almost three weeks, as early as a few nights before the full moon and up to two weeks later. Additionally, gametes were absent from a variable proportion of colonies in approximately half the species observed to spawn in March, and from all colonies in an additional 13 species, suggesting they either did not spawn during that year or were likely to spawn during a different season. Slicks of spawn have also been observed at the Abrolhos in February, although subsequent sampling suggested the bulk of the community was likely to spawn in March. The species known to spawn during months other than March on more northern reefs were either not sampled, or had a proportion of colonies without eggs and were sampled in low replication. There is currently no reproductive information for brooding corals, which are likely to release planulae over several months from spring to autumn, but with perhaps a reduced reproductive window due to cooler water temperatures.

### **Regional patterns of coral reproduction: Southwest Region**

Within the temperate southwest region of WA, corals are near their geographical limit. Reefs where corals are known to occur include Rottnest Island, Hall Bank, and some patches of reef within lagoons adjacent to the Perth mainland, such as at Marmion and Jurien. Rottnest Island has the most abundant coral communities, with 25 species from 16 genera. *Pocillopora damicornis* dominates certain areas (Veron & Marsh, 1988), which is a consequence of clonal reproduction (Stoddart, 1984). Clonal reproduction may also be important for other species at Rottnest Island with more tropical affinities,

such as *Acropora* sp. and *Porites lutea* (Crane, 1999). Among the remaining corals, the dominant taxa are species of Faviidae with subtropical affinities, such as *Goniastrea australiensis*. Macroalgae (*Sargassum* and *Ecklonia*) are common around Rottneest Island and contribute up to 60% of benthic cover (Wells & Walker, 1993). Between Rottneest Island and the Perth metropolitan coastline is Hall Bank, a small reef with a low diversity (14 spp.) but a high cover ( $\approx 50\%$ ) of corals, of which most are *Favites* and *Goniastrea* (Thomson & Frisch, 2010). In contrast, the reefs adjacent to the coastline have a lower coral diversity and cover, such as Marmion lagoon with 10 species from eight genera (Veron & Marsh, 1988). Fleshy macroalgae are dominant on most of the temperate reefs, but corals are often found among the algae in low density (Thomson et al., 2012). The most abundant coral on these reefs is *Plesiastrea versipora*, one of the Indo Pacific's most widespread corals, however it rarely reaches large sizes and other species tend to have higher cover (e.g. *Goniastrea* spp. *Montipora capricornis*).

Throughout the southwest region, coral reproduction has been investigated only at Rottneest Island during one or more years throughout the 1980s and (Table S1). At Rottneest Island, a total of nine species and > 600 colonies were sampled over multiple seasons, for months to years (Table 1). The majority of the sampling has been conducted at two sites, which includes consecutive sampling and spawning observations of colonies prior to spawning around summer and autumn from January–May. Histological analyses were also used to investigate reproduction in three species (*Pocillopora damicornis*, *Alveopora fenestrata* and *Porites lutea*) from December–April. Mature gametes were found in colonies of the most abundant spawning corals over several months through summer and autumn (Tables 2 and S2). Histological analyses revealed *Pocillopora damicornis* at Rottneest Island to be both a brooding and spawning coral. Gametes and planula larvae were common in colonies through summer to winter (December to early April), being most common in March, and rare or absent in winter.

The available data for the southwest region are only from Rottneest Island where spawning by the dominant species appears to occur through summer and or autumn months (e.g. *Goniastrea aspera*, *G. australensis*, *Montipora mollis* and *Symphyllia wilsoni*), a pattern similar to that seen on the subtropical reefs of Australia's east coast. Some colonies have been observed to spawn around the time of new moon rather than full moon, such as *Symphyllia wilsoni*, and *Alveopora fenestrata*. Among the other dominant coral species in the region, there appears to be an extended reproductive season of two or more months at different times of year for different corals; for example, in summer for *Pocillopora damicornis*, in early autumn for *Turbinaria mesenterina*. The apparent staggering of reproduction among species between February and May suggests that there is a relatively low level of synchrony within the temperate coral communities, but with perhaps a higher degree of synchrony among some conspecific colonies in late summer (Table S2). Because the species composition and level of coral cover varies so markedly among coral assemblages in the southwest, there is little or no knowledge of spatial variation in community reproduction throughout the region. For example, *Plesiastrea versipora* is numerically the most common coral in the region and across southern Australia, yet its reproductive biology in temperate waters is still poorly understood.

It is recorded as a mass spawner on tropical reefs (Magnetic Island, [Babcock et al., 1986](#); Taiwan, [Dai, Soong & Fan, 1992](#)), but did not spawn with other subtropical corals such as *G. australiensis* in Moreton Bay, on the east coast of Australia ([Fellegara, Baird & Ward, 2013](#)). There is no knowledge of the distribution and patterns of reproduction in brooding corals through the southwest region, with the exception of *Pocillopora damicornis* at Rottneest Island.

## DISCUSSION

### Summary of coral reproduction across Western Australia

The observed differences in reproduction among Western Australian (WA) coral reefs are due to their varying community composition, modes of reproduction, and the cycles of gametogenesis for coral species. The most obvious differences in community composition are the higher abundance and diversity of Acroporidae and massive *Porites* on offshore reefs and tropical reefs north of the Abrolhos Islands. Among the inshore reefs and those south of the Abrolhos Islands, species of Faviidae, Pocilloporidae, *Turbinaria* and/or *Pavona* are more common and there is a notable decline in the abundance and diversity of coral species ([Lough & Barnes, 2000](#); [Speed et al., 2013](#); [Veron & Marsh, 1988](#)). Beyond the effect of community composition, the modes of reproduction displayed by the different coral species distinguished their cycles of gametogenesis and times of reproductive output.

As on most tropical reefs around the world, the dominant mode of coral reproduction on WA coral reefs is broadcast spawning. Within a year, most individual corals have a single cycle of gametogenesis that culminates in spawning during one or a few consecutive nights each year. However, the times of spawning and the degree of synchrony among and within species vary among the different regions, with a latitudinal gradient in the spawning activity among seasons. The primary period of spawning on all WA reefs (apart from the southwest region) is in autumn, often culminating in the mass spawning of a relatively high proportion of species and colonies during March and/or April.

Successive studies have added to the list of species known to mass spawn during autumn, but also to the list known to participate in a second multi-specific spawning during spring (October and/or November) on many WA reefs. The existing data suggest that biannual spawning by communities during autumn and spring is a phenomenon that occurs with increasing frequency from Ningaloo Reef north. Although more intensive sampling is necessary to clearly establish a latitudinal gradient, synchronous spawning by multiple species and colonies in the spring spawning is highest on the Kimberley Oceanic reefs, decreases considerably on Pilbara reefs, and may not occur on Ningaloo reefs—there is only anecdotal evidence of multi-specific spawning at Ningaloo Reef in spring. Of the 17 species of biannual spawners on the Kimberley Oceanic reefs that were sampled most rigorously in the other regions of WA, all spawned in autumn and five during spring in the Pilbara, and all spawned in autumn and none during spring at Ningaloo ([Table 2](#)). In addition to the reduction in spring spawning with increasing latitude, spawning may also become more protracted over consecutive nights or weeks

around the mass spawning in autumn from reefs in the Kimberley to the Abrolhos Islands (Table 2), although more data are again required to confirm this pattern.

Within these seasons, there is a comparatively poor understanding of spatial and temporal variation in spawning times (months, weeks, time of day). Mass spawning occurs most commonly in March and/or April, and the multi-specific spawning in October and/or November, often varying according to the timing of the full moon. As with coral communities on the Great Barrier Reef, spawning on WA reefs can be split over consecutive months in autumn and spring, depending on the timing of the full moon. The phenomenon typically occurs every few years, but can also occur in consecutive years. The nights of spawning were typically inferred from the presence of pigmented eggs in colonies days to weeks before the predicted dates, with very few direct observations of spawning and limited sampling conducted after the event. There is certainly a peak in spawning activity (mass spawning) over a few nights each year on most reefs, but with a variable participation by colonies and species in this primary spawning event. Most commonly, mass spawning occurs during neap tides between approximately 7–12 nights after the full moon, usually in March and/or April, on all reefs but for those in the temperate southwest region. However, intensive sampling of colonies over days and weeks at Ningaloo Reef has also documented spawning around the time of the new moon, as can occur in some species on the GBR (Babcock *et al.*, 1986). Whether this pattern reflects a more protracted spawning that is unique to Ningaloo Reef, or is a feature of other WA reefs remains to be determined.

Despite some brooding corals being widely distributed and abundant on many of WA's coral reefs (e.g. species of Pocilloporidae and *Isopora*), there is currently little information about their cycles of gametogenesis and times of planulae release. Within a year, brooding corals on WA reefs probably have multiple cycles of gametogenesis culminating in the release of planulae larvae over several months, similar to those on the GBR (Harriott, 1983b; Harrison & Wallace, 1990; Kojis, 1986; Tanner, 1996; Wallace *et al.*, 2007). On the Kimberley Oceanic reefs, planulae were present within *Isopora brueggemanni* and *Seriatopora hystrix* during several months through spring to autumn. Brooding corals on other WA reefs probably have similar cycles of planulation, but for perhaps a shorter reproductive window on higher latitude reefs. The relative proportion of planulae produced during different months of the year and the nights of their release relative to the phases of the moon are unknown for all brooding corals on all reefs.

### Methods for assessing coral reproduction

Consideration of coral reproduction is often required by environment managers where development activities are proposed on or near coral reefs; the principle being that if coral spawning and larval settlement are concentrated during a discrete period then the potential impacts from development works can be minimised. Rigorous sampling and interpretation of reproductive status in coral communities is needed well in advance to provide time for planning; sampling is also needed to continue throughout to confirm predictions about time(s) of spawning. In all cases, the accurate prediction of the timing,

magnitude and duration of coral spawning is vital given the logistical complexity of development operations and the cost of delays.

Many early studies of coral reproduction employed rigorous, and often complimentary, methods because so few data existed. The resulting publications provided a detailed description of the methodology and the assumptions on which conclusions were based. Attempts to quantify cycles of reproduction today require a good knowledge of this background literature, and particularly the limitations of the different approaches. The most relevant literature and methods for a particular study will depend on the questions to be addressed, the regions in which the reefs are found and the species to be investigated. However, to maximise the knowledge gained and minimise the biases from sampling effort, many publications should first be read and understood; for example: *Alino & Coll, 1989; Ayre & Resing, 1986; Done & Potts, 1992; Fadlallah, 1983; Fan & Dai, 1995; Fong & Glynn, 1998; Glynn et al., 1994; Glynn et al., 1991; Harrison, 1993; Harrison & Wallace, 1990; Heyward & Collins, 1985; Sakai, 1997; Sebens, 1983; Shlesinger, Goulet & Loya, 1998; Stoddart, 1983; Stoddart & Black, 1985; Szmant-Froelich, Reutter & Riggs, 1985; Szmant & Gassman, 1990; Wallace, 1985*. In the context of environmental management, we provide some comments on the experimental design and methodology used in coral reproductive studies in Western Australia, which also provides some background to a thorough reading of the existing literature.

### ***Community composition***

For environmental management, information about coral reproduction is often required at the level of the entire community. Thus, there is a need to assess the composition of coral communities across the susceptible reefs, habitats and sites, in order to quantify the relative dominance of the species. As the species list of corals at tropical reefs can be extensive, a convenient cut-off point must be chosen. Therefore, we suggest that the species be ranked in terms of their contribution to total coral cover, and those making a cumulative contribution to most ( $\approx 80\%$ ) cover across all communities of interest be chosen for assessment of reproductive behaviour. However, consideration must also be given to whether certain species, although low in relative abundance, play a critical role in ecosystem maintenance (e.g. keystone species).

### ***Taxonomic resolution***

Coral taxonomy and the identification of species for sampling are problematic in virtually any study of tropical coral communities; the issue cannot be understated. Identification to the finest taxonomic resolution possible is always desirable; however, the suggested approach of quantifying seasonal reproductive patterns for dominant taxa would work equally well for higher taxonomic groups. For example, a more practical approach depending on the diversity of species and the taxonomic skills of the researchers would be to group species according to a higher taxonomic level (e.g. Genus, Family) and to also consider growth form (e.g. massive, branching, encrusting, corymbose) and reproductive mode (spawner, brooder). The advantage with this approach is that uncertainty around the identity of species is obvious, rather than records of incorrectly

identified species becoming entrenched in the literature. Such approaches are valid where the objective of management is to protect reef integrity by ensuring resilience of the coral assemblage at a functional level.

### ***Inferring spawning and timing of sampling***

Sampling of the dominant corals must take place throughout the potential reproductive seasons in order to determine the relative magnitude of reproductive output throughout the year. A key factor in the logical process of determining whether or not spawning has taken place is the construction of a series of data points through time that demonstrates the development of gametes and their subsequent disappearance after spawning. Oogenic cycles in spawning corals take several months, so in species known to spawn biannually (March, October) or over a protracted period (September–April) eggs will be present in the population during most months. There is no evidence of corals spawning during winter months, so detailed sampling in this period is not necessary. A sampling program to determine the proportion of species and colonies spawning or releasing planulae throughout the year should, however, span at least nine months from the start of spring to the end of autumn.

Preliminary sampling should be conducted monthly, and take into consideration the influence of the lunar cycles. Ideally, sampling on Western Australian reefs should occur approximately one week before the predicted night of spawning, providing the greatest amount of information on the timing of spawning based on characteristics of gamete development; more than a week and eggs may not yet be pigmented, while less than a week the chances of missing an early spawning increases. The optimal time of sampling will depend on the assemblage. The presence of mature (pigmented) eggs or larvae (in brooding species), and fully developed sperm, followed by their subsequent disappearance, is the best basis for making strong inferences about the timing of spawning. It is important to note that in many corals, particularly the Acroporidae, eggs may not be pigmented more than two weeks prior to spawning and that unpigmented eggs may also be spawned, highlighting the need for large sample sizes and for sampling to be conducted following spawning events. In other taxa, particularly some Faviidae, eggs may be pigmented for two months or more before spawning.

A single annual sample is a weak basis for inference, particularly when spawning is split or staggered, for species that have protracted spawning seasons, or for brooding corals. It is vital that accurate records of the exact timing of sampling are reported as metadata, in order for clear conclusions to be drawn regarding the timing of spawning based on sequential sampling.

In addition to re-sampling the assemblage through time, tagged colonies would ideally be resampled to strengthen inferences about the time(s) of spawning. This eliminates doubt about whether the presence or absence of gametes is due to a spawning event, or due to variation in the timing of spawning among colonies within a population; it is particularly useful for species that spawn biannually. Consideration must obviously be given to the number of samples that can be taken from a single colony, so as not to cause significant stress and divert energy investment away from reproduction. We suggest that samples from

individual colonies are therefore taken strategically, according to the wider pattern identified in the population from which random samples are also taken. For example, sampling an individual colony to determine whether it participates in both a spring and autumn spawning, or in both months of a split spawning, rather than during many months of the year.

### **Sample size**

Sample sizes must be adequate for the purposes of the study and to account for the background variation in reproduction among species within the community, among conspecific colonies during a year, and among years. If all colonies are reproducing and spawn during the same month, then the level of replication required is small—but considerable sampling is first required to establish this trend and it is uncommon for many species on most reefs. Relying on a fixed sample size for all species can become problematic when colonies spawn during different months, different seasons, if stressed colonies are not reproducing, if they have separate sexes, or if spawning during a year is split. Simulations carried out to assess the power of sampling to detect reproductively mature colonies in coral communities (*Styan & Rosser, 2012*) can provide useful guidelines for designing sampling programs, after the underlying assumptions have been reviewed and the background variance established in the context of the assumptions of the simulation. The required replication can range from a few colonies per species when all spawn synchronously over a few nights each year, to many more colonies for assemblages with mixed patterns of reproduction during some years. For example, on a reef when 30% of the assemblage is spawning in spring, many colonies per species will need to be sampled following the full moon in October during a year of split-spawning (after the October spawning) so as not to underestimate the significance of the event, especially if a proportion of colonies are not reproducing due to environmental stress. Otherwise, insufficient sampling would not identify the period as important and it may not be investigated in subsequent years when spawning was not split and colonies not stressed.

It is important to note that the absence of eggs in a colony provides few insights into broader patterns of reproduction, further highlighting the need for sufficient replication. At least 10 or more colonies per species are therefore needed for adequate quantification of reproductive patterns on WA reefs that do not mass spawn during a single month each year—however, the replication required on each reef can only be determined after background variation in space and time are first established. We argue that for most WA reefs it is better to first sample the most abundant species rigorously to determine their pattern of reproduction, rather than sample most species within low replication. Additionally, within colonies not all polyps may be reproductive, so multiple samples from single colonies are advisable. For example, where both in situ and microscopic examination of eggs are used to infer times of spawning in certain coral species (e.g. staghorn *Acropora*), eggs may be observed in one method but not the other.

### **Use of existing data and streamlining of sampling**

Studies based on the sampling design principles above are rare, not only in WA but globally due to logistical demands. However, they are necessary for environmental

managers because there is insufficient knowledge of the underlying reproductive biology of seasonality and within-population synchrony in coral species at any given location. Where there is well documented information on seasonality and synchrony, sampling may be streamlined. For example, when the species' annual gametogenic cycle has been described and it has been shown that the population spawned with virtually 100% synchrony during one lunar period of the year, sampling could be conducted immediately before and after the predicted spawning window. However, for most species of coral in WA such information is lacking, making more extended sampling periods necessary.

Once the community has been defined and the experimental design confirmed, methods that can be used to determine the time of spawning or planulae release include: spawning observations, recruitment to artificial substrata, in situ examination of gametes, microscopic examination of gametes (immediate and preserved), and histological examination of gametes. The most appropriate method depends on the question to be addressed, the region in which the reefs are found and species being investigated, but a rigorous assessment usually combines multiple approaches.

### ***Direct observations***

Direct observations to establish the date and time of spawning include those made of colonies in situ or in aquaria (e.g. [Babcock, Willis & Simpson, 1994](#)). In situ observations are the most reliable way to confirm spawning, but are rarely conducted because the logistic difficulties limit replication. The most useful way to apply in situ spawning observations is therefore to combine them with data from previous reef surveys and in situ observation of gamete development (see below). Aquarium observations present similar logistical issues, and inflict some level of stress on colonies that potentially alters their time of spawning. The approach has been used more successfully in brooding corals kept in aquaria for several months, with the dates of planula release around lunar phases determined each day with the use of planula collectors (e.g. [Richmond & Jokiel, 1984](#); [Jokiel, Ito & Liu, 1985](#)).

Another observational method used to provide information on the timing of spawning in coral communities is visual surveys for coral spawn slicks, usually the morning after a spawning event. While this method is useful for establishing that some spawning has occurred, the approach cannot provide information on the scale of the spawning and the origin of the slicks is unknown; the absence of a slick obviously provides no evidence of spawning having not occurred. While all of these methods provide information about the time of spawning in a sub-set of species, they alone are not sufficient to establish the community-wide patterns of reproductive seasonality required for the purposes of managing environmental impacts.

### ***Coral recruitment***

Coral recruitment surveys can be used to inform the general timing of peaks in reproduction (months/seasons) ([Wallace & Bull, 1982](#)) but they do not precisely describe temporal variation in peaks in reproduction. This is in part because pre-settlement larval periods vary among coral, particularly spawning and brooding corals, and artificial

substrata must be deployed and retrieved in a set period ( $\approx$  few weeks) before and after each spawning; the period before is required to pre-condition substrata with algal communities and the period after is required for larval metamorphosis and calcification to occur. Deploying and retrieving substrata each month is logistically difficult and provides indirect, and relatively imprecise, information about coral reproduction. A more precise identification of spawning times is usually required by environmental managers. The link between coral reproduction and recruitment can also be decoupled by unknown rates of larval mortality, current speeds and directions (Caley *et al.*, 1996; Edmunds, Leichter & Adjeroud, 2010; Hughes *et al.*, 2000) and recruitment provides retrospective rather than predictive insights into the times of reproductive output.

### ***In situ examination of eggs***

In situ examination of eggs is the most common and perhaps useful means of determining times of spawning, provided certain criteria are met. If knowledge of the proportion of colonies participating in a spawning event is required it is vital to know whether the species are hermaphroditic or gonochoric (separate sexes), as eggs will obviously be absent from male colonies. Eggs of gonochoric species are often small and relatively colourless (Harrison & Wallace, 1990). Even where gonochoric species produce large coloured eggs, testes will remain colourless or white and difficult to distinguish from the white skeleton of a coral fragment. The sex ratio of gonochoric species must be known if the presence of mature (pigmented) eggs in colonies is to be used to infer the proportion spawning. Thus, in situ visual examination of gonochoric species is more difficult and likely to lead to incorrect conclusions. It is also vital not to sample the sterile tips or the edges of a colony, which have grown subsequent to the initiation of gametogenesis in the rest of the colony (Oliver, 1984; Wallace, 1985). Furthermore, it is very important to examine multiple polyps within each sample, and multiple samples from each colony, as some polyps may be sterile or have low fecundity. These points apply to whatever method of oocyte examination is to be employed.

In situ examination of eggs is most useful for branching corals that have large ( $\approx > 0.5$  mm) pigmented oocytes prior to ( $< 2$  weeks) spawning that can be easily identified in the field (e.g. *Acropora* spp.). Colonies are generally examined in situ several days prior to the predicted dates of spawning. Maturity is examined in the field by breaking off coral sections to expose oocytes (Harrison *et al.*, 1984), and several sections should be examined if eggs are not initially observed. Oocyte pigmentation is often used as an indication of maturity and timing of imminent spawning. Egg colour varies with developmental stage from small unpigmented eggs (indicating spawning is still some months away), to large pigmented eggs. Importantly, the size of mature eggs and the degree and colour of pigmentation varies among species; when mature *Acropora* eggs are typically pink or red, whereas the Faviidae may be blue or green, the *Montipora* may be brown due to the presence of zooxanthellae, while other species may have cream eggs when mature (Babcock *et al.*, 1986; Harrison & Wallace, 1990; Heyward & Collins, 1985; Shlesinger, Goulet & Loya, 1998). In *Acropora*, pigmentation may not occur

until two weeks or less before spawning, in some Faviidae eggs may be pigmented as much as two months before spawning, and species such as *Acropora* and massive *Porites* have been observed to spawn unpigmented eggs ([Babcock et al., 1986](#); [Harrison et al., 1984](#); [Harrison & Wallace, 1990](#); [Mangubhai & Harrison, 2007](#); [Stoddart, Stoddart & Blakeway, 2012](#)), all complicating the use of egg colour as an indicator of imminent spawning. While in situ visual observations have led to many useful inferences about the timing of spawning in coral communities, they can be ambiguous and are best used as part of a sampling program that also uses microscopic examination of eggs, and ideally the sequential sampling of tagged colonies. Spawning times should also be confirmed by the disappearance of eggs from colonies following the predicted date of spawning.

### ***Microscopic examination of gametes***

In situ examination of polyps is well supported by microscopic examination of the samples on the same day. Such examinations should be conducted on broken sections of coral under a dissecting microscope or with a hand lens, and can reveal gonads that were not visible underwater. This is particularly useful for species with small polyps and gonads, or those with a low fecundity (e.g. branching *Acropora*). Inferences about the times of spawning are also improved by investigating the developmental stages of testes. When testes are prepared and examined with a compound microscope (40× objective), sperm shape and motility can be observed. Testes enlarge markedly and sperm develop tails during the last month before spawning. Sperm heads remain spherical until the last one to two weeks before spawning, when they will become cone or acorn shaped, and a high degree of sperm motility occurs a few days before spawning ([Harrison et al., 1984](#)). Microscopic examinations are more time consuming, but always more reliable and informative than field observations alone.

Microscopic examination of gamete development can also be conducted on well preserved samples, but only after the sample has been decalcified with acid. Egg colour and shape are not retained following preservation and it is not possible to discern aspects of sperm morphology or behaviour. Where the dimensions of mature eggs or testes are known for species being sampled, measurements of their size can be used to make inferences about the likely time of spawning. Several studies have quantified the size of eggs within replicate colonies of a species at the time of spawning, and there can be variation in egg sizes within colonies and among conspecific corals ([Gilmour et al., 2016](#); [Heyward & Collins, 1985](#); [Mangubhai, 2009](#); [Mangubhai & Harrison, 2007](#); [Stobart, Babcock & Willis, 1992](#); [Wallace, 1985](#); [Wallace, 1999](#)). Egg size prior to spawning can also vary considerably from year to year, and is not a reliable metric alone for determining the month of spawning. Therefore, egg size can be used to estimate level of maturity and as an indicator of spawning with accuracy of perhaps two months, but probably not for a single month or less. Consequently, investigation of the preserved gametes is particularly useful for tracking their development over several months leading up to a spawning event, but to determine the month(s) spawning also requires in situ and microscopic examination as part of the sequential sampling program.

### ***Histological examination of gametes***

Histology is used for corals that are not well suited to field examinations, usually due to their morphology and their having small polyps and eggs that are not easily visible with the naked eye (i.e. massive *Porites*, *Pavona*). Often these are also gonochoric species with separate male and female colonies, for which histology provides the only approach to describing the development of testes prior to spawning. This method is also commonly employed to assess reproductive status of brooding corals and the presence of planula larvae. Preparation for histological examination is time consuming and costly, and usually involves decalcifying tissue, dehydration and fixing of samples in wax, and then sectioning and mounting tissue to slides. Egg and testis development or presence of planula larvae can then be assessed using previous work as guides (*Szmant-Froelich, Reutter & Riggs, 1985; Vargas-Ángel et al., 2006*). The development and growth of gonads and gametes can be tracked by measuring changes in size as well as morphological developmental features like sperm shape through time. As with in situ examination of gonads, sperm development stage is a particularly useful indicator of maturity and imminent spawning. Gamete development stages are frequently used in describing the reproductive status of corals sampled using histological methods, and also occasionally for microscopic examinations of freshly sampled tissues. Gamete development staging should be done with reference to published and accepted staging criteria available in the peer reviewed literature, and clearly defined so that the unambiguous interpretation of staging by others will be possible.

### ***Complementary methods***

The most informative studies of coral reproduction involve sequential sampling of colonies using a combination of complementary methods. For example, determining the times of spawning may involve monthly examination of eggs in preserved samples. As eggs approach a size in which spawning is likely, then preserved samples may be supplemented or replaced by in situ and microscopic examination of egg size and pigmentation, as well as the size of testes and the stages of sperm development. When the night of spawning is predicted within a given month, the in situ and microscopic examinations of eggs and sperm are continued on a daily basis around the predicted nights of spawning, possibly supplemented by in situ observations of spawning and evidence of spawn slicks the following day. On all reefs, a proportion of species and colonies typically spawn over several nights, so continued sampling is required to quantify the proportion of colonies without eggs and to identify the main night of mass spawning within a period.

Great care should be taken to correctly record metadata and to correctly identify the main night of spawning relative to the full moon, particularly to note instances when split-spawning has occurred. Split-spawning typically occurs every few years and can occur over consecutive years, and not recognising the phenomenon has biased the existing data for Western Australian reefs. Also, supplementing these methods with tagged colonies that are sampled periodically through time will give a better indication of whether split-spawning has occurred, whether assemblages spawn biannually or

over a protracted period, or whether species have overlapping gametogenic cycles (e.g. *Turbinaria*). For gonochoric species with small polyps and gametes, or brooding corals, this sampling approach will likely involve the use of histological analyses as well as in situ and microscopic methods. These approaches are examples of applying multiple complimentary methods, but the best approach will depend on the aims of the study, the region, habitat, and species being investigated.

### **Quantifying temporal variation in coral reproductive output**

Since the discovery of mass coral spawning on the Great Barrier Reef, the phenomenon of mass- or multi-specific spawning has been documented at an increasing number of reefs around the world (*Baird, Guest & Willis, 2009; Harrison, 2011*). In many of these studies sampling has been conducted around the main periods of spawning on the nearest reefs and focused on species of *Acropora*, which are most likely to spawn synchronously and are easiest to sample. The results have established the timing and participation by species in the primary spawning event(s). However, fewer studies have provided detailed information about cycles of gametogenesis in spawning corals and planulation in brooding corals during other months of the year, despite a proportion of colonies of some of the most common species not participating in the primary spawning event(s) on a reef. For example, on inshore reefs of Western Australia's Pilbara region the *Acropora* may be relatively rare ( $\approx 5\%$  by cover), whereas species of massive *Porites*, *Turbinaria* and *Pavona* that have novel cycles of reproduction may be among the most common (10–20% by cover) (*Baird et al., 2011; Stoddart, Stoddart & Blakeway, 2012*). Even on reefs where the *Acropora* are among the most common genera (25% by cover), such as on the oceanic reefs of the Kimberley, other common groups of corals such as the massive *Porites* (20%), *Isopora* (14%) and Pocilloporidae (10%) also have different reproductive modes or cycles.

An accurate assessment of the significance of periods of reproductive output requires knowledge of the proportion of colonies within each species releasing gametes or larvae during many months of the year. Additionally, several years of data with varying environmental conditions are required to understand the drivers of inter-annual variation, such as whether a low participation in a spawning event was due to environmental stress or split-spawning. Without these comprehensive data, surveys during previous years provide few insights into future spawning events, requiring substantial sampling effort to be repeated prior to every period of interest. In the worst instances, focusing only on the participation by species in a single month risks perpetuating a paradigm of mass spawning or missing a significant period of reproductive output.

A lack of accurate and unbiased information about times of reproductive output by coral communities impedes management initiatives aimed at reducing pressures to their early life history stages. Managers would ideally be provided with quantitative estimates of the reproductive output during different weeks, and even nights of the year, and its contribution to the long-term maintenance of populations. Obtaining this knowledge is logistically impossible until methods are developed that can easily quantify larval production, survival, connectivity, and per capita rates of recruitment per adult,

for the most abundant species within a community. However, with far less effort it is possible to obtain relative estimates of reproductive output for coral communities in different months of the year. Mass spawning was originally defined as ‘... the synchronous release of gametes by many species of corals, in one evening between dusk and midnight...’ (Willis *et al.*, 1985), taking place within a mass spawning period of up to a week following full moon on the Great Barrier Reef. There has since been debate about what constitutes a ‘mass spawning’ or a ‘multi-specific spawning’ on a reef, and a quantitative estimate of spawning synchrony has been developed (Baird, Guest & Willis, 2009) to assess biogeographic variation in spawning synchrony among species. Here we consider one approach to quantifying the significance of periods of reproductive output for coral communities on a reef, which combines the relative abundance of coral groups with the proportion spawning or releasing larvae during different months.

To apply information on reproductive synchrony to the management of ecological processes, such as reproduction and recruitment in coral communities, it is necessary to quantitatively weight this information according to community composition. Community composition on a reef varies considerably among habitats (lagoon, reef flat, reef crest, reef slope) and among sites within these habitats, particularly on inshore reefs. The abundance of corals with different cycles and modes of reproduction also vary among these habitats and sites, so careful consideration must be made of the assemblage of corals that best characterises the reef when assessing its times of reproductive output (or the assemblage for which reproductive information is required). Here we define the community based on percentage cover data, which is regularly collected during monitoring programs across habitats and replicate sites. These data provide a less biased sample of the community composition than is often obtained during reproductive surveys and can provide unexpected insights into which coral groups are most common and whether their patterns of reproduction are well known. For example, knowledge of coral reproduction is often for the most conspicuous and easily sampled species of *Acropora*, whereas little reproductive data may exist for other species of spawning (e.g. *Montipora*, *Porites*) and brooding corals (e.g. *Isopora*, *Seriatopora*) that may have a similar relative abundance on a reef.

Once the community composition has been quantified, a decision must be made about whether all taxa are to be included, or whether sampling effort can be reduced by excluding the rare corals. Although there are typically over tens of genera and hundreds of coral species on tropical coral reefs, many species are rare. For example, on Kimberley oceanic reefs there are over 35 genera and 300 species of hard corals, but 10 genera contribute approximately 85% of the coral cover and five genera contribute approximately 65% of the cover. On reefs with less diversity, comparatively few species may contribute much of the coral cover. A ‘community’ may therefore be defined by the corals that make up most (e.g. > 80%) of the total coral cover. An alternative to using a threshold of relative abundance is applying multivariate analyses to quantify the coral groups that best characterise, or distinguish, community structure through space and time, depending on the objectives of the study. Focusing on the detailed patterns of reproduction in the dominant species on a reef significantly reduces the sampling effort

required to quantify temporal variation in reproductive output, as finding and sampling rare species with sufficient replication is most time consuming. Care must obviously be taken in deciding the threshold for including dominant species in a 'community' and the means by which they are categorised (e.g. family, genus, species, growth form), which will need to be reviewed as communities change and as more reproductive data are obtained.

Further confounding assessments of the significance of reproductive periods on a reef is the identification of coral species. The issue is improved by considering only the most common species, but even these can be very difficult to distinguish. Variation in physical conditions among reefs and habitats, hybridization, reproductive isolation, and cryptic speciation make it impossible to correctly identify all of the colonies sampled during extensive reproductive surveys, and very few people are capable of correctly identifying most colonies correctly in situ. For example, many species of *Porites*, Faviidae, *Montipora* and *Acropora* are common on most tropical coral reefs, but within each of these taxa are many species easily confused in situ, even by experts. Errors in the identification of species will affect estimates of the number of species and the proportion of their colonies participating in a spawning, yet this can be the criteria by which the significance of spawning events is assessed. Inconsistent identification of species likely accounts for some apparent discrepancies in the times of spawning by species within regions of Western Australia presented here.

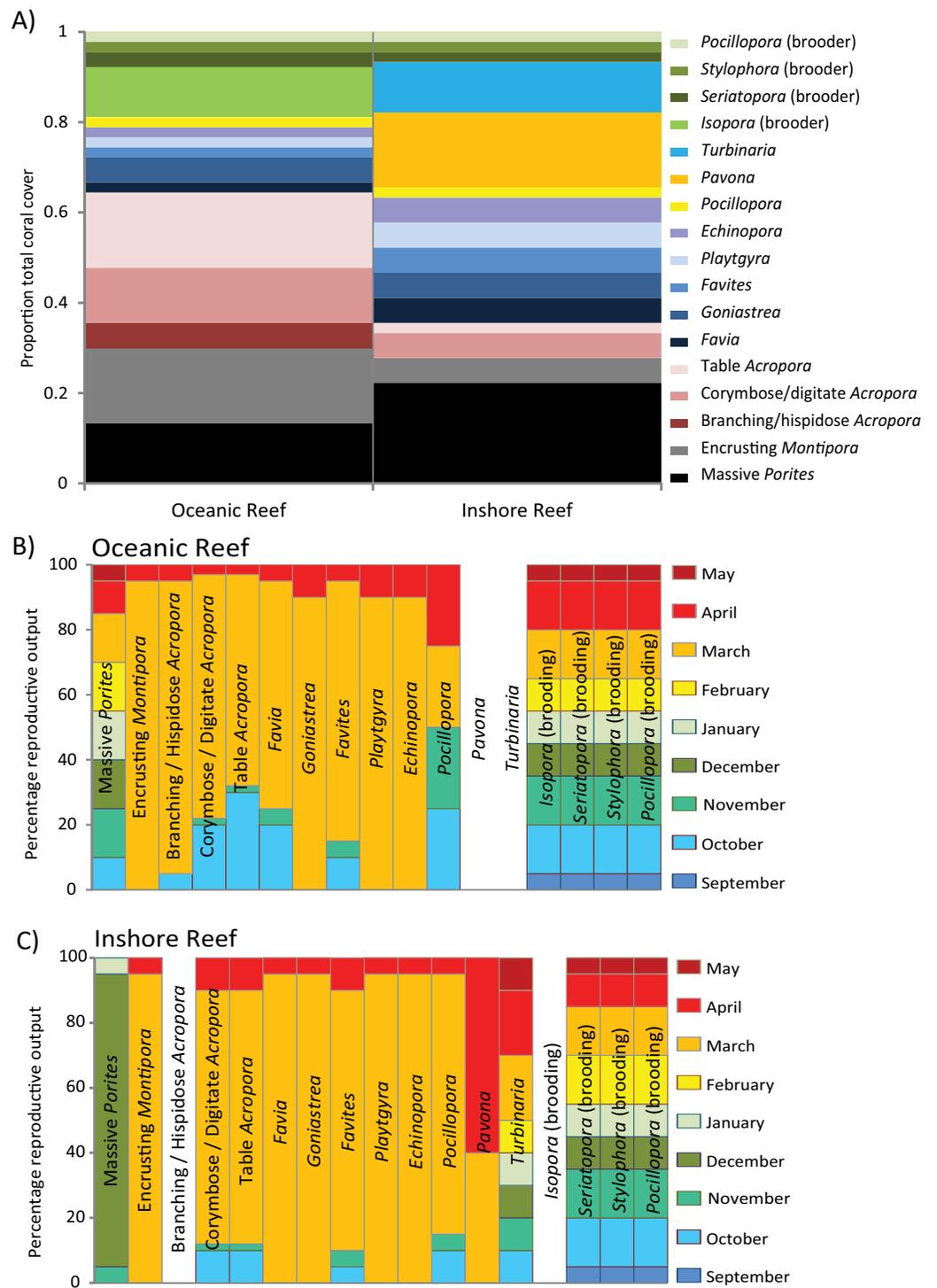
It is also impossible to correctly identify all species when quantifying the composition of coral communities in monitoring programs, particularly from photographic or video stills. Broader taxonomic, morphological and life history groups are usually used in this context. Thus, when quantifying the significance of spawning events for coral communities, errors can be avoided and efficiency increased by grouping some species to a higher taxonomic level (Genera/Family), but also distinguishing these according to growth form (e.g. branching, corymbose, encrusting; Wallace, 1999; Veron, 2000) and reproductive mode (spawner, brooder; Harrison & Wallace, 1990; Baird, Guest & Willis, 2009). The approach is obviously not needed for species that are abundant and/or functionally important on a reef and easily identified (e.g. *Isopora brueggemanni*, *Seriatopora hystrix*, *Diploastrea heliopora*).

Once the community of interest is defined and the relative cover of coral groups determined, the patterns of reproduction must be accurately quantified (see Results). The approach suggested here is to combine the community abundance and reproductive data to quantify relative estimates of reproductive output by the community throughout the year; it is therefore necessary to have both types of data for the same groups of corals. For example, in a hypothetical coral assemblage of two species, species A makes up 20% (relative) of the total coral cover and spawns only during October, and species B makes up 80% of the coral cover and spawns during March. Reproductive output for the community is therefore 20% during October and 80% in March. In this example, both species reproduce exclusively during a single month, whereas communities characteristically have species that spawn during two or more months a year, due to phenomena such as split-spawning, asynchronous spawning and within-population

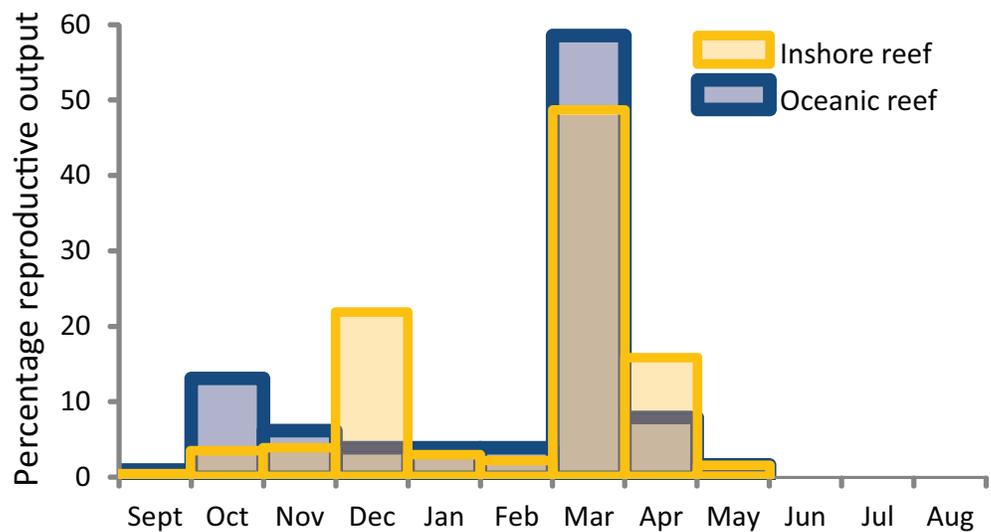
biannual spawning. Additionally, brooding corals release larvae over several months within a year. Here we use available data to apply the approach at two *hypothetical* reefs with contrasting coral assemblages and patterns of reproduction (Fig. 2), which are similar to those at some oceanic and inshore reefs of Western Australia. The method for calculating reproductive output during each month is simple (Table S4), but considerable sampling effort is required to produce accurate estimates of community composition and the proportion of colonies within each taxa reproducing each month (see Results; Table S4). Quantifying the proportion reproducing each month will usually require monthly sampling, or at least bimonthly, although less effort may be required after several years under a range of conditions and depending on the methods used.

In a hypothetical example for an oceanic and inshore reef at north-western Australia, the monthly reproductive output differed according to their community composition and the cycles of reproduction within and among coral taxa (Fig. 3). The main month of reproductive output at both reefs was March, but with more synchronous spawning in March at the oceanic reef and more protracted spawning over March and April at the inshore reef. At both reefs, over 40% of the communities reproductive output occurred during other months, but for different reasons. The oceanic reef had a higher ( $\approx 20\%$ ) reproductive output during spring (October/November) and particularly October than at the inshore reef ( $\approx 8\%$ ), due to a higher number of species spawning biannually, a higher abundance of *Acropora*, and a tendency for spawning to be more synchronous during a single month. There was a much higher reproductive output in December (22%) on the inshore reef, due to the abundance many massive *Porites* that spawn predominantly in December. During several other months of the year reproductive output was higher on the oceanic reef, due mainly to the many massive *Porites* spawning and brooding *Isopora* releasing larvae from spring to autumn. In contrast, the brooding corals in this example were rare on the inshore reef and the spawning over several months was restricted to the *Turbinaria*. These estimates of reproductive output for the oceanic reef and the inshore reef are hypothetical, intended only to provide a worked example.

This is one of several possible approaches to quantifying temporal variation in reproductive output for an entire community throughout the year, intended to aid management decisions. The approach is aimed at identifying the months in which significant reproductive output occurs at the scale of the entire community, and more detailed temporal sampling within these months is required to determine the nights of spawning and planula release relative to the phases of the moon. In the context of managing environmental impacts, the approach presented here has several limitations. Most significantly, by considering the reproductive output of the community as a whole, it does not sufficiently recognise the significance of periods of reproductive output by functionally important species with unique cycles of reproduction. For example, massive *Porites* on inshore reefs that spawn predominantly just a few nights after the full moon in December (Stoddart, Stoddart & Blakeway, 2012), or species on the oceanic reefs that may spawn exclusively during spring (Table S4). Additionally, brooding corals may have a negligible (e.g.  $< 20\%$ ; Table S4) proportion of planula release during the month and



**Figure 2** Variation in composition and times of reproduction at Western Australian reefs. (A) Proportional contribution of coral groups to total coral cover at a hypothetical oceanic and inshore reef, and the percentage reproductive output (spawning, planula release) through the year at the (B) oceanic and (C) inshore reef. In this example, *Pavona* and *Turbinaria* were absent from the oceanic reef and *Isopora* absent from the inshore reef.



**Figure 3** Percentage reproductive output during each month on a hypothetical oceanic and inshore reef at north-western Australia. Calculations are based on the relative abundance of coral groups within the community and the proportion reproductive output for spawning and brooding corals during each month of the year (Fig. 3; Table S4).

particularly main night of mass spawning on a reef, occurring around the full moon over several other months through the year.

Importantly, the proportion of reproductive output each month will vary among years according to changes in community structure and particularly the occurrence of split-spawning or environmental stress. Consequently, several years of data collection are required to obtain a reasonable understanding of reproduction on the reef before sampling effort can be reduced. For example, it may be concluded incorrectly that reproductive output was not significant during March, the usual month of mass-spawning by coral on most Western Australian reefs, if spawning was split (March/April) or because environmental stress (e.g. poor water quality, cyclone damage or mass-bleaching) precluded reproduction. Another limitation of this approach is that the temporal resolution is presented to the calendar month, with the assumption that spawning occurs approximately one week after the full moon, whereas reproductive output in some spawning corals (e.g. Faviidae at Ningaloo Reef) and many brooding corals are likely to occur around the new moon. Furthermore, affording protection to only the main month of mass spawning and not in other months may have unforeseen consequences, such as affecting connectivity between reefs following spawning events in which oceanographic currents differ (Gilmour, Smith & Brinkman, 2009), or by reducing the genetic diversity of new recruits. This highlights the need to consider reproductive output for the entire community in the context of more detailed reproductive data for abundant or functionally important species of corals. Assessing the strengths and weaknesses of the approach requires a dedicated sampling design, on reefs with different coral communities through several years of environmental conditions. Other (and possibly better) approaches exist; however we present one here to formally introduce and hopefully build the concept.

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The authors declare that they have no competing interests.

### Author Contributions

- James Gilmour conceived and designed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Conrad W. Speed analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Russ Babcock conceived and designed the experiments, wrote the paper, reviewed drafts of the paper.

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**SUPPLEMENTARY TABLE 1. SOURCES OF CORAL REPRODUCTIVE DATA FOR REGIONS ACROSS WESTERN AUSTRALIA**

Data were sourced from public journal articles and reports, plus confidential reports written by private consultants and provided by government and industry. Raw data were not available for all reports and text and derived data within reports were used to contribute to the regional summaries.

<b>Region</b>	<b>Publication</b>
<b>Kimberley Oceanic</b>	<p>Gilmour, J., Smith L. D., et al. (2009). Biannual spawning, rapid larval development and evidence of self-seeding for scleractinian corals at an isolated system of reefs. <i>Marine Biology</i> 156: 1297-1309.</p> <p>Gilmour, J. P., Travers M. J., et al. (2011). Long-term monitoring of coral and fish communities at Scott Reef. SRRP Project 1 Final Report for Woodside Energy as operator of the Browse LNG Development. Perth, Western Australia, Australian Institute of Marine Science. 157pp.</p> <p>Gilmour J.P., Underwood J.N., Howells E.J., Gates E., and Heyward A.J. (2016). Biannual Spawning and Temporal Reproductive Isolation in <i>Acropora</i> Corals. <i>Plos one</i> 11:11(13): e0150916. doi:0150910.0151371/journal.pone.0150916.</p> <p>Heyward, A. J., Jones, R. J. <i>et al.</i> (2012). Monitoring study S6B Coral Reefs, Montara: 2011 Shallow reef surveys at Ashmore, Cartier and Seringapatam Reefs. Final Report for PTTEP Australiasia (Ashmore Cartier) Pty. Ltd. Australian Institute of Marine Science, Townsville. 163pp.</p> <p>Heyward, A. J., Radford. B. <i>et al.</i> (2013). Seringapatam Reef Baseline Surveys 2012-2013. Final Report for Conoco Philips (Browse Basin) Pty Ltd. Australian Institute of Marine Science, Perth 2013. 117pp.</p>
<b>Kimberly Oceanic, Ningaloo</b>	<p>Rosser, N. (2013). Biannual coral spawning decreases at higher latitudes on Western Australian reefs. <i>Coral Reefs</i> 32(2): 455-460.</p>
<b>Kimberley</b>	<p>INPEX (2011). Biological and ecological studies of the Bonaparte Archipelago and Browse Basin. Perth, INPEX - Ichthys Project.</p>
<b>Kimberley, Pilbara</b>	<p>Rosser, N. and Baird A. H. (2009). Multi-specific coral spawning in spring and autumn in far north-western Australia. <i>Proc 11th Int Coral Reef Sym.</i> 1:366-370.</p>

Region	Publication
<b>Pilbara</b>	<p>Baird, A. H., Blakeway D., <i>et al.</i> (2011). Seasonality of coral reproduction in the Dampier Archipelago, northern Western Australia. <i>Marine Biology</i> 158: 275-285.</p> <p>Mscience (2007). Pluto LNG Development - Spawning Assessment October 2007, Report No. MSA93R3.</p> <p>Mscience (2008). Pluto LNG Development - Spawning Assessment March 2008, Report No. MSA93R22.</p> <p>Mscience (2009). Pluto LNG Development - Spawning Assessment February 2009, Report No. MSA93R78.</p> <p>Mscience (2009). Pluto LNG Development - Spawning Assessment March 2009, Report No. MSA93R85.</p> <p>Mscience (2009). Pluto LNG Development - Spawning Assessment April 2009, Report No. MSA93R92.</p> <p>Mscience (2009). Pluto LNG Development - Re-assessment of Spring 2008 Spawning in <i>Porites</i>, Report No. MSA93R104.</p> <p>Mscience (2009). Pluto LNG Development - Porites Spawning Assessment – Summer 2009, Report No. MSA93R126.</p> <p>SKM (2011). Cape Lambert Port B Development Dredging Marine Environmental Monitoring - Coral Spawning Assessment Summary Report - February Spawning Window, Rev 1 WV05051-FI-RS-001, March 2011.</p> <p>SKM (2011). Cape Lambert Port B Development Dredging Marine Environmental Monitoring - Coral Spawning Assessment Summary Report - March Spawning Window, Rev 0 WV05051-FI-RS-0002, March 2011.</p> <p>SKM (2011). Cape Lambert Port B Development Dredging Marine Environmental Monitoring - Coral Spawning Assessment Summary Report - October Spawning Window, Rev 0 WV05051-FI-RS-0003, October 2011.</p> <p>SKM (2011). Cape Lambert Port B Development Dredging Marine Environmental Monitoring - Coral Spawning Assessment Summary Report - November Spawning Window, Rev 0 WV05051-FI-RS-0004, November 2011.</p> <p>SKM (2011). Cape Lambert Port B Development Dredging Marine Environmental Monitoring - Coral Spawning Assessment Summary Report - December Spawning Window, Rev A WV05051-FI-RS-0005, December 2011.</p> <p>SKM (2012). Cape Lambert Port B Development Dredging Marine Environmental Monitoring - Coral Spawning Assessment Summary Report - February Spawning Window, Rev 0 WV04505-FI-RS-0001, February 2012.</p> <p>SKM (2012).Cape Lambert Port B Development Dredging Marine Environmental Monitoring - Coral Spawning Assessment Summary Report, March Spawning Window, Rev 0 WV04505-FI-RS-0002, March 2012.</p>

Region	Publication
<b>Pilbara</b>	<p>SKM (2010). Proposed Outer Harbour Development Port Hedland - Coral spawning spring surveys 2009 Revision B - WV03716-MV-RP-0041 04, June 2010.</p> <p>SKM (2010). Proposed Outer Harbour Development Port Hedland - Coral spawning Autumn surveys 2009 Revision 0WV03716-MV-RP-0034 2, September 2009.</p> <p>Simpson, C. J. (1985). Mass spawning of scleractinian corals in the Dampier Archipelago and the implications for management of coral reefs in Western Australia. Perth, Western Australia, Department of Conservation and Environment. 224: 35pp.</p> <p>Stoddart, J. A. and J. Gilmour (2005). Patterns of reproduction of in-shore corals of the Dampier Harbour, Western Australia, and comparisons with other reefs. Corals of the Dampier Harbour: Their Survival and Reproduction During the Dredging Programs of 2004. S. E. Stoddart. Perth, MScience Pty Ltd. 53-64.</p> <p>Stoddart C, Stoddart J, Blakeway D (2012). Summer spawning of <i>Porites lutea</i> from north-western Australia. <i>Coral Reefs</i> 31:787-792.</p> <p>Rosser, N. L. and J. P. Gilmour (2008). New insights into patterns of coral spawning on Western Australian reefs. <i>Coral Reefs</i> 27(2): 1-5.</p>
<b>Pilbara, Ningaloo</b>	<p>Rosser, N. L. (2005). Reproductive seasonality and biannual spawning of <i>Acropora</i> on two north-west Australian reefs. Murdoch University. Western Australia. 125pp.</p>
<b>Ningaloo</b>	<p>Gilmour J. 1999. Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral. <i>Marine Biology</i> 135:451-462.</p> <p>Heyward A.J., Smith L.D., Rees M., and Field S.N. (2002). Enhancement of coral recruitment by in situ mass culture of coral larvae. <i>Marine Ecology Progress Series</i> 230:113-118.</p> <p>Smith, R. A. (1993). Mass Spawning in the <i>Faviidae</i> on the Ningaloo Reef Tract. Perth, Western Australia, Murdoch University. 126pp.</p> <p>Stewart, R. R. (1993). Mass Spawning in the <i>Acroporidae</i> on the Ningaloo Reef Tract. Science. Perth, Western Australia, Murdoch University. 94pp.</p> <p>Taylor J.G., and Pearce A.F. (1999). Ningaloo Reef currents: implications for coral spawn dispersal, zooplankton and whale shark abundance. <i>Journal of the Royal Society of Western Australia</i>. 82: 57-65.</p>

<b>Region</b>	<b>Publication</b>
<b>Abrolhos Islands</b>	<p>Babcock, R. C., B. Willis, et al. (1994). Mass spawning of corals on a high latitude coral reef. <i>Coral Reefs</i> 13: 161-169.</p> <p>Dinsdale E.A., and Smith L. D. (2004). Broadscale survey of coral condition on the reefs of the Easter Group of the Houtman Abrolhos Islands. Report the Western Australian Department of Fisheries. 23pp.</p> <p>Foster T., Gilmour J.P., et. al. (2015). Effect of ocean warming and acidification on the early life stages of subtropical <i>Acropora spicifera</i>. <i>Coral Reefs</i>: 1-10.</p>
<b>Southwest</b>	<p>Crane, K. R. (1999). Reproductive Biology of Scleractinian Coral at Rottnest Island, Western Australia. Marine Department. Perth, Murdoch University: 160.</p>

## SUPPLEMENTARY TABLE 2. REGIONAL VARIATION IN SPAWNING FOR CORAL SPECIES ON WESTERN AUSTRALIAN REEFS

Seasons and months in which coral species are thought to spawn based on the available data; evidence for some species is likely biased by issues with identification and methodology. Species do not spawn during all months below in every year, but have been inferred to spawn in the months below during one or more years. For example, the primary month of spawning on many reefs during autumn is March and during spring is October, but spawning can also occur in April and November due to split-spawning or a late full moon during some years. Similarly, within species an equal proportion of colonies do not spawn during each month. For example, in species that spawn during autumn and spring across Western Australia, a higher proportion of colonies typically spawn during autumn. Regions are colour coded according to Figure 1. Seasons and months are: Spring (Spr), September (s), October (o), November (n); Summer (Sum), December (d), January (j), February (f); Autumn (Aut), March (m), April (a), May (m). Spawning has not been recorded during Winter months (June, July, August) in Western Australia and they have been excluded. Species names are presented as per the original literature and taxonomic revisions are in Supplementary Table 3.

Based on the available data, the sampling design and the methods used, confidence in the inferred months of spawning was ranked qualitatively according to:

- 1** Confident. Evidence based on the presence of pigmented eggs in colonies prior to the predicted dates of spawning in many colonies, sites and years; the presence and absence of pigmented eggs in many colonies around the predicted dates of spawning; and/or direct observations of spawning in multiple colonies.
- 2** Likely. Evidence based on the presence of pigmented eggs in many colonies prior to the predicted dates but with limited spatial and temporal replication; and/or most evidence indicates spawning during this month but with some contradictory data among studies.
- 3** Possible. Evidence based on the presence of large but unpigmented eggs several weeks prior to the predicted dates of spawning; and/or contradictory data among studies due to sampling design, methodology or species identification.
- 4** Unlikely. No evidence of spawning; pigmented or large unpigmented eggs absent from samples of many colonies, sites and years within several weeks of the predicted dates of spawning.



















### SUPPLEMENTARY TABLE 3. TAXONOMIC REVISIONS.

There have been a number of significant taxonomic revisions of hard corals in recent years (Arrigoni et al. 2014; Benzoni et al. 2007; Budd et al. 2012; Hoeksema 1989; Huang et al. 2014; Huang et al. 2011; Kitano et al. 2014; Wallace 1999; Wallace et al. 2012). Subsequently, species and genera have been synonymised and re-classified. Reproductive data in Supplementary Table 2 are based on species names used in the original literature, but have been updated here according to the World Register of Marine Species (WORMS) (Appeltans et al. 2012).

Reference name	WORMS nomenclature	Authority
<i>Acropora formosa</i>	<i>Acropora muricata</i>	(Linnaeus 1758)
<i>Acropora danai</i>	<i>Acropora abrotanoides</i>	(Lamarck 1816)
<i>Acropora stoddarti</i>	<i>Acropora divaricata</i>	(Dana 1846)
<i>Acropora tumida</i>	<i>Acropora valida</i>	(Dana 1846)
<i>Alveopora fenestrata</i>	<i>Acropora yongei</i>	(Veron and Wallace 1984)
<i>Barabattoia amicorum</i>	<i>Dipsastraea amicorum</i>	(Milne Edwards & Haime 1849)
<i>Echinophyllia lamellosa</i>	<i>nomen dubium</i>	nomen dubium
<i>Favia chinensis</i>	<i>Euphyllia glabrescens</i>	(Chamisso and Eysenhardt 1821)
<i>Favia danae</i>	<i>Dipsastraea danai</i>	(Milne Edwards 1857)
<i>Favia fавus</i>	<i>Dipsastraea fавus</i>	(Forskål 1775)
<i>Favia maritima</i>	<i>Dipsastraea maritima</i>	(Nemzo 1971)
<i>Favia matthaii</i>	<i>Dipsastraea matthaii</i>	(Vaughan 1918)
<i>Favia maxima</i>	<i>Dipsastraea maxima</i>	(Veron, Pichon & Wijzman-Best 1977)
<i>Favia pallida</i>	<i>Dipsastraea pallida</i>	(Dana 1846)
<i>Favia rotumana</i>	<i>Dipsastraea rotumana</i>	(Gardiner 1899)
<i>Favia speciosa</i>	<i>Dipsastraea speciosa</i>	(Dana 1846)
<i>Favia stelligera</i>	<i>Goniastrea stelligera</i>	(Dana 1846)
<i>Favia truncatus</i>	<i>Dipsastraea truncata</i>	(Veron 2000)
<i>Favia veroni</i>	<i>Dipsastraea veroni</i>	(Moll & Best 1984)
<i>Favites bennettiae</i>	<i>Oulophyllia bennettiae</i>	(Veron Pichon & Best 1977)
<i>Favites russelli</i>	<i>Paragoniastrea russelli</i>	(Wells 1954)
<i>Goniastrea australensis</i>	<i>Paragoniastrea australensis</i>	(Milne Edwards 1857)
<i>Montastraea curta</i>	<i>Astrea curta</i>	(Dana 1846)
<i>Montastraea magnistellata</i>	<i>Favites magnistellata</i>	(Chevalier 1971)
<i>Montastrea curta</i>	<i>Astrea curta</i>	(Dana 1846)
<i>Mycedium mankaoi</i>	<i>Mycedium mancaoii</i>	(Nemzo 1979)

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## SUPPLEMENTARY TABLE 4. REPRODUCTIVE OUTPUT AT A HYPOTHETICAL OCEANIC AND INSHORE REEF OF WESTERN AUSTRALIA

Percentage cover and reproductive data were applied to 17 coral groups that together accounted for most (90%) of the total coral cover at each reef. Quantification of community composition was based on percentage cover estimates derived from replicate sites and habitats within the region of interest. The relative abundances of coral groups were calculated as the percentage cover of each group divided by the total coral cover, and are relevant until disturbances or succession cause major changes in composition. Quantification of the monthly reproductive output was based on the random sampling of species and colonies within each coral group, which weights/biases estimates for the group according to the relative abundance of the species within. The times of reproductive output for spawning corals were inferred from a combination of presence of eggs of different development stages following visual inspection of fragments *in situ* and with a dissection microscope, and some observations of coral spawning; the times of planulae release by brooding corals were based on histological analyses revealing the presence of gametes of varying stages of development and the presence of planulae larvae in visual assessments of colony fragments *in situ* and with a dissection microscope. The reproductive output of each coral group during each month was multiplied by its relative cover within the community. The reproductive output for each coral group during each month was then summed to calculate the total monthly reproductive output. The approach is aimed at identifying the months in which significant reproductive output occurs at the scale of the entire community, and more detailed temporal sampling within these months is required to determine the nights of spawning and planula release, relative to the phases of the moon.





## SUPPLEMENTARY TEXT 1. REGIONAL VARIATION IN ENVIRONMENTAL CONDITIONS ON WESTERN AUSTRALIAN REEFS

### **Kimberley Oceanic Region**

The oceanic reefs in the Kimberley region ( $\approx 12^{\circ}\text{S}$  -  $17.5^{\circ}\text{S}$ ) of north-western Australia are isolated atolls rising from depths of several hundred meters near the edge of the continental shelf, more than 200 km from the coastline and from each other (Berry & Marsh 1986; Veron & Marsh 1988a; Wilson 2013). The dominant oceanic feature is the Indonesian Throughflow, which transports warm low salinity water into the region through the Indonesian Archipelago (Cresswell et al. 1993; Domingues et al. 2007; Holloway 1995). The Indonesian Throughflow also provides a mechanism for the transport of pelagic larvae from the Pacific and Southeast Asian reefs to north-western Australia, so the fauna at the oceanic atolls have a closer affinity to Indonesian reefs than to others in Western Australian waters. The local oceanography is influenced by semi-diurnal tides of up to approximately 5 m, and the waters around the reefs are warm, clear and nutrient deficient. Mean seawater temperatures vary seasonally, from a low of approximately  $26^{\circ}\text{C}$  in winter to maxima of approximately  $30^{\circ}\text{C}$  during December and March, with a small drop in mid-summer due to monsoonal cloud cover and storm activity.

The distance of the reef systems from the mainland means they are not affected by terrestrial runoff and associated issues of degraded water quality. There is also relatively little fishing pressure at the reefs, with the notable exception of traditional fishing by Indonesians for shark fin, *Trochus* and sea cucumber at some reefs (Stacey 2007), and/or some managed professional and recreational fishing. The most frequent disturbance to these reefs is seasonal storms and cyclones. Severe monsoonal winds and waves impact the reefs from a west, south-westerly direction between November and April, with cyclone impacts occurring through a similar period (Berry & Marsh 1986; Bowman et al. 2010). Since 1998, elevated water temperatures are known to have caused moderate to severe coral bleaching. Coral bleaching caused the mass mortality of corals at Scott Reef in 1998 (Gilmour et al. 2013), and less extreme temperature anomalies have caused moderate bleaching events at all the reefs during the last decade. Outbreaks of coral predators and disease have not been recorded, apart from a small outbreak of disease that affected some corals at parts of Scott Reef in 2010. However, most of the reproductive data collected from the oceanic atolls were not biased by these disturbances.

## **Kimberley Region**

The Kimberley region ( $\approx 12^{\circ}\text{S} - 17.5^{\circ}\text{S}$ ) of north-western Australia includes a vast network of fringing and coastal reefs, spanning over 4000 km of open coast and a coastline of over 13000 km (Short 2011; Wilson 2013). The oceanography is influenced by similar regional currents as the oceanic reefs, but with a more local influence of the Holloway Current adjacent to the shelf edge (D'Adamo et al. 2009; Wilson 2013). The local oceanography is dominated by a diurnal tidal range of up to 10 m, which coupled with strong currents and shallow bathymetry can cause periods of extreme turbidity on some reefs (Richards et al. 2014; Wilson 2013). Mean seawater temperatures are slightly higher than on the oceanic reefs, varying from approximately  $25^{\circ}\text{C}$  in July to  $31^{\circ}\text{C}$  in March. The coastal zone is characterised by extensive intertidal reefs, mudflats, mangrove forests, and muddy shorelines (INPEX 2011).

The remoteness of the Kimberley means it is currently not affected by degraded water quality or significant fishing pressure, although the region is of increasing economic importance and coastal developments are planned (Keesing et al. 2011). The most frequent disturbances to the region are monsoonal storms and cyclones through January to April (Veron & Marsh 1988a). There are no reports of outbreaks of coral disease or predators, or of temperature induced mass-bleaching events, but the remoteness of the region means there have been few surveys of the coral communities. However, the little reproductive data collected from the Kimberley region are unlikely to have been biased by disturbances.

## **Pilbara Region**

The Pilbara region ( $\approx 19^{\circ}\text{S} - 21^{\circ}\text{S}$ ) of Western Australia has extensive and varying coral reef habitats, ranging from highly turbid, sheltered reefs along the mainland to wave exposed fringing reefs on mid-shelf islands (Blakeway & Radford 2004; Veron & Marsh 1988b; Wilson 2013). The regional oceanography reflects a zone of transition from the dominant currents in the Kimberley region, particularly the Holloway Current, to the region in which the Leeuwin Current intensifies to the north of Ningaloo reef. As with the Kimberley, the longshore, wind-driven currents of the Pilbara region are linked to the seasonal changes in winter tradewinds and summer monsoonal storms, but are dominated locally by relatively

large (5 m) semi-diurnal tides and the complex topography of the mainland and island archipelagos (Wilson 2013). Water temperature within the inshore area has the largest seasonal range in Western Australia, of between 20 to 30° C, and can reach as high as 34° C in late summer (Jones 2004). High concentrations of plankton, organic detritus and particulate sediments result in high turbidity at the inshore reefs, which is further elevated by the shallow bathymetry, tidal range, strong currents, and resuspension of sediments by seasonal winds, storms and cyclones (Jones 2004).

The tropical, semi-arid climate within the Pilbara is punctuated by high temperatures, sporadic rainfall, and frequent tropical cyclones between December and April (Jones 2004). Damage from tropical cyclones is significant, causing some of the highest historical wind gusts recorded in Australia. Associated with these storms are the localised impacts of freshwater run-off from the mainland and islands. More recently, temperature induced coral bleaching has caused severe, and in places repeated, damage to Pilbara reefs. Coral bleaching and mortality was first observed in the Dampier Archipelago in 1998, and since 2008 coral bleaching has been reported on reefs adjacent to the mainland at Dampier and Onslow, in the Dampier Archipelago, and around Barrow and Montebello Islands (Chevron 2014; Moore et al. 2012; MScience 2010; Speed et al. 2013). Additionally, outbreaks of the coral eating snail (*Drupella cornus*) and particularly the crown-of-thorns starfish (*Acanthaster planci*) have been reported periodically on Pilbara reefs, and have caused severe impacts at some sites within the Dampier Archipelago (Wilson 2013). In addition to these more regional scale disturbances, some reefs within the Pilbara experience additional pressure from recreational fishing and industrial developments, particularly within Mermaid Sound and in the west Pilbara. Mermaid Sound is the site of a major industrial port servicing resource development in the northwest of Australia (Hanley 2011) and in the west Pilbara major gas developments with associated port infrastructure are located around the mainland at Onslow and Barrow Island. Considerable research and monitoring efforts have been carried out to document marine flora and fauna around these developments, with an emphasis on effects of elevated turbidity and sedimentation from dredging operations (e.g. Rosser & Baird 2009; Stoddart et al. 2012; Stoddart & Gilmour 2005). Many of the inshore coral reefs of the Dampier Archipelago are naturally turbid, with increases in turbidity and sedimentation in recent decades generated by port dredging, so the current coral assemblages are likely to be relatively tolerant to these conditions. In contrast, reefs in the outer archipelago are naturally less turbid, which is reflected in their coral assemblages. Port developments and dredging

operations have more recently altered water quality on reefs in the west Pilbara. The cumulative impacts of these operations and background impacts from cyclones and coral bleaching have in recent years reduced cover and diversity, increased susceptibility of assemblages to diseases, and reduced rates of coral growth, survival and recruitment (Chevron 2014; Pollock et al. 2014). These disturbances have biased at least some of the coral reproductive data collected from the Pilbara region.

### **Ningaloo Region**

Ningaloo Reef ( $\approx 21.5^{\circ}\text{S} - 23.5^{\circ}\text{S}$ ) is the largest continuous reef system in Western Australia. The reef system consists of approximately 300 km of barrier and fringing reefs (Veron & Marsh 1988a), with reef passages connecting the offshore waters to the extensive back-reef and lagoon. The dominant oceanographic feature in the region is the Leeuwin Current, which intensifies around Ningaloo Reef as the southward flow of warm water in autumn and winter (Cassata & Collins 2008; Holloway & Nye 1985), and disperses tropical larvae to subtropical reefs. However, this is countered by the northern flow of the Ningaloo Current adjacent to the coastline from spring to winter, a process that can produce upwelling events that cool the waters on the western side of Northwest Cape during the summer (Taylor & Pearce 1999; Woo et al. 2006). Relatively small, semi-diurnal tides of up to approximately 2 m have little influence on the regional oceanography. Mean monthly sea surface temperatures vary seasonally, from a low of approximately  $23^{\circ}\text{C}$  in late winter and early spring, to a high of approximately  $28^{\circ}\text{C}$  in late summer and the early autumn months. Ningaloo Reef has a unique fauna, but with some affinities to the Pilbara reefs to the north and those in the region of Shark Bay and the Abrolhos Islands to the south (Veron & Marsh 1988a). Affinities with Pilbara reefs are particularly strong for reefs such as Bundegi, located on the eastern side of Northwest Cape, which experience greater environmental variability and higher turbidity and sedimentation. The outer reef edge is surrounded by clear oceanic water and subjected to heavy wave action, with a strong flow of water over the reef flat.

There are no major industrial or port developments in the region of Ningaloo, and the lack of major river systems means the reefs are not affected by terrestrial runoff and the associated issues of degraded water quality. There are commercial fishing operations in the region and also recreational fishing pressure. One of the most common disturbances is severe storms and tropical cyclones, usually approaching from a north-westerly direction from November to

April. In recent years, recurrent temperature anomalies have also affected Ningaloo Reef, and in the summer of 2010-2011 parts of the reef suffered severe impacts from a combination of a coral bleaching and cyclone (Depczynski et al. 2013; Moore et al. 2012). There are few records of outbreaks of coral disease or the predatory crown-of-thorns starfish, but outbreaks of the coral-eating snail *Drupella* have been reported periodically (Black & Johnston 1994; Holborn et al. 1994). However, these disturbances are unlikely to have biased the existing data on coral reproduction for the region.

### **Abrolhos and Shark Bay Region**

The Abrolhos Islands ( $\approx 28^{\circ}\text{S}$  -  $29^{\circ}\text{S}$ ) are the most southerly accretive reef formations in the Indian Ocean, comprising four island groups that are near the continental shelf edge (Veron & Marsh 1988a). Situated to the north of the Abrolhos Islands, Shark Bay ( $\approx 26^{\circ}\text{S}$ ) is a large shallow bay ( $\sim 12,950 \text{ km}^2$ ) enclosed by a number of islands, with an average depth of 9 m (Veron & Marsh 1988a). The bay consists of vast seagrass meadows (Wells et al. 1985) and localised coral communities, but few data on coral cover and community composition exist (but see Bancroft 2009; Cary 1997; Moore et al. 2011). The distribution and diversity of reefs in the region are probably facilitated by the Leeuwin current, which brings warm waters and coral larvae from the north during autumn and winter following the main period of spawning at Ningaloo Reef (Hatcher 1991; Hutchins & Pearce 1994; Taylor & Pearce 1999). Water temperatures during winter are therefore relatively warm, ranging seasonally between  $20^{\circ}\text{C}$  and  $25^{\circ}\text{C}$  (Pearce 1986; Veron & Marsh 1988b). The seaward reefs of the Abrolhos are exposed to strong wave action and have extensive areas of algal growth, whereas most coral communities occur in back reef areas and form patches in western lagoons (Veron & Marsh 1988a).

The reefs at Shark Bay and the Abrolhos Islands are not currently impacted by major industrial or port developments, nor terrestrial runoff, and typically have high water quality. Despite being located at relatively high latitudes, however, the flow of warm water with the Leeuwin Current has caused temperature anomalies and coral bleaching at the Abrolhos in 2011 (Abdo et al. 2012). The Abrolhos Islands have a targeted fishery of western rock lobster (*Panulirus cygnus*), the most valued single-species fishery in Australia (Caputi et al. 1996). The effect of the fishery and the removal of biomass on the ecosystem is inconclusive (Bellchambers 2010), but other commercial developments may have some impact on the

coral reefs in the region (e.g. Oceanica & MScience 2006). The limited existing data on coral reproduction at the Abrolhos Islands is unlikely to have been biased by disturbances.

### **Southwest Region**

The South West region ( $\approx 30^{\circ}\text{S}$  -  $33^{\circ}\text{S}$ ) includes temperate reef patches around the Perth metropolitan area (e.g. Hall Bank and Marmion lagoon), at Rottnest Island 20km off the coastline, and 250km north of Perth in Jurian Bay. Hard corals are ubiquitous on the temperate limestone reefs along the coast of the region (Thomson et al. 2012), but with a mean cover of less than few percent (Speed et al. 2013). Areas where corals form more significant components of the benthic assemblages are rare and are restricted spatially, most commonly on the leeward side of islands or in bays and lagoons where they are sheltered from the westerly winds and waves generated by winter storms (Hatcher 1989; Veron & Marsh 1988a). The dominant oceanographic influence for the coral reefs around Rottnest Island is the southerly flow of warm tropical water through autumn and winter with the Leeuwin Current (Veron & Marsh 1988a). However, the Leeuwin Current has less influence on the reef patches and lagoons adjacent ( $< 3$  km) to the Perth Metropolitan area, which experience lower water temperatures and higher turbidity due to terrestrial runoff (Harriott & Banks 2002; Thomson & Frisch 2010).

Marine habitats surrounding Rottnest Island and Hall Bank are exposed to extensive wave energy during winter storms (Wells & Walker 1993). Although rarely documented, coral bleaching due to high temperature anomalies has affected both shallow and deep water coral communities around Rottnest Island (Thomson et al. 2011). In addition, the corals in the metropolitan area are also exposed to pressures related to urbanization and infrastructure development, such as terrestrial runoff, dredging and port development, and recreational and commercial fishing (SKM 2011). However, the reproductive data available for the southwest region are unlikely to have been biased by disturbances.

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