# Coral reproduction in Western Australia

James Gilmour, Conrad W Speed, Russ Babcock

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

1 **Coral reproduction in Western Australia**

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11 ABSTRACT

12      Larval production and recruitment underpin the maintenance of coral populations, but these

13 early life history stages are vulnerable to extreme variation in physical conditions.

14 Environmental managers aim to minimise human impacts during significant periods of larval

15 production and recruitment on reefs, but doing so requires knowledge of the modes and timing of

16 coral reproduction. Most corals are hermaphroditic or gonochoric, with a brooding or broadcast

17 spawning mode of reproduction. Brooding corals are a significant component of some reefs and

18 produce larvae over consecutive months. Broadcast spawning corals are more common and

19 display considerable variation in their patterns of spawning among reefs. Highly synchronous

20 spawning can occur on reefs around Australia, particularly on the Great Barrier Reef. On

21 Australia's remote north-west coast there have been fewer studies of coral reproduction. The

22 recent industrial expansion into these regions has facilitated research, but the associated data are

23 often contained within confidential reports. Here we combine information in this grey-literature

24 with that available publicly to update our knowledge of coral reproduction in WA, for tens of

25 thousands of corals and hundreds of species from over a dozen reefs spanning 20 degrees of

26 latitude. We identified broad patterns in coral reproduction, but more detailed insights were

27 hindered by biased sampling; most studies focused on species of *Acropora* sampled over a few

28 months at several reefs. Within the existing data, there was a latitudinal gradient in spawning

29  activity among seasons, with mass spawning during autumn occurring on all reefs (but the

30  temperate south-west). Participation in a smaller, multi-specific spawning during spring

31  decreased from approximately one quarter of corals on the Kimberley Oceanic reefs to little

32  participation at Ningaloo. Within these seasons, spawning was concentrated in March and/or

33  April, and October and/or November, depending on the timing of the full moon. The timing of

34  the full moon determined whether spawning was split over two months, which was common on

35  tropical reefs. There were few data available for non-*Acropora* corals, which may have different

36  patterns of reproduction. For example, the massive *Porites* seemed to spawn through spring to

37  autumn on Kimberley Oceanic reefs and during summer in the Pilbara region, where other

38  common corals (e.g. *Turbinaria* & *Pavona*) also displayed different patterns of reproduction to

39  the *Acropora*. The brooding corals (*Isopora* & *Seriatopora*) on Kimberley Oceanic reefs

40  appeared to planulate during many months, possibly with peaks from spring to autumn; a similar

41  pattern is likely on other WA reefs. Gaps in knowledge were also due to the difficulty in

42  identifying species and issues with methodology. We briefly discuss some of these issues and

43  suggest an approach to quantifying variation in reproductive output throughout a year.

## INTRODUCTION

46  **Reproduction in scleractinian corals**

47  Sexual recruitment underpins the maintenance of most coral communities, so knowing their peak

48  times of reproductive output is critical to the management of human activities that reduce

49  recruitment to the adult population. Larval production, recruitment, and early post-recruitment

50  survival in corals are reduced by extreme variation in physical factors such as temperature and

51  salinity (Bassim et al. 2000; Harrison et al. 1990; Harrison 2011; Negri et al. 2007) or degraded

52  water quality (Gilmour 1999; Harrison & Ward 2001; Humphrey et al. 2008; Markey et al. 2007;

53  Negri & Heyward 2001). Model projections highlight the implications of prolonged reductions in

54  larval recruitment for the maintenance of coral populations, and particularly their recovery

55  following disturbances (Babcock 1991; Done 1987; Edmunds 2005; Fong & Glynn 2000;

56  Gilmour et al. 2006; Smith et al. 2005). The times of reproduction also influence the community

57  recovery via connectivity to other coral reefs (Gilmour, 2009, Done, 2015). For example, the

58  larvae of brooding corals are released several times a year under a range of hydrodynamic

59  conditions, but typically disperse over relatively short distances (< several kilometres), whereas

60  the larvae of spawning corals are produced during one or a few discrete periods, and disperse

61  over larger distances (> several kilometres). A detailed understanding of community

62  reproduction is therefore required to mitigate human activities around critical periods of larval

63  production and to inform the design of management networks reliant on estimates of larval

64  exchange (Carson & al 2010; Kool et al. 2013).

65  Most scleractinian corals have one of four patterns of sexual reproduction, depending on their

66  sexuality (hermaphroditic or gonochoric) and developmental mode (brooding or broadcast

67  spawning) (Baird et al. 2009; Fadlallah 1983; Harrison et al. 1990; Harrison 2011; Richmond &

68  Hunter 1990). In brooding corals, the fertilisation of eggs and subsequent development of larvae

69  occur within the parental polyps. Larvae are competent to settle shortly after their release from

70  the polyp, with planulation typically occurring over several months each year. In contrast,

71  colonies of broadcast spawning corals typically release their gametes into the water column once

72  a year, where fertilization and larval development occur, after which larvae disperse for days to

73  weeks before settling. Some coral species (or cryptic sub-species) have more complex patterns of

74  reproduction (e.g. *Pocillopora damicornis*), while blurred species boundaries and flexible

75  breeding systems continue to confound our understanding of reproduction in many coral taxa

76  (van Oppen et al. 2002; Veron 2011; Willis 1990; Willis et al. 2006).

77  Reproductive activity in spawning corals can be remarkably synchronised, culminating in the

78  release of gametes by a high proportion of species and colonies during a few nights each year

79  (mass spawning), or spawning by a similar proportion of colonies and species may be protracted

80  over many nights and several months (Baird et al. 2009; Harrison et al. 1990; Harrison 2011).

81  The ultimate factor driving high synchrony, particularly within species, is probably successful

82  fertilisation and larval recruitment. However, a wide range of environmental factors underlie this

83  success and cue spawning over increasingly fine temporal scales, such as water temperature, day

84  length, moon phases and tidal amplitude (Baird et al. 2009; Guest et al. 2005a; Harrison et al.

85  1990; Penland et al. 2004; van Woesik 2010). These cues all interact to synchronise spawning

86  within communities, so it is tempting to view mass spawning as a phenomenon that occurs at the

87  community level, whereas each species is in fact responding independently to its environment.

88  As conditions vary, gametogenic cycles in each species will respond differently, as their

89    environmental optima may differ or because the environment provides fewer synchronising cues

90    (Oliver et al. 1988). Indeed, environmental stress will reduce the energy available for

91    gametogenesis and the likelihood of corals reproducing during a given year (Michalek-Wagner

92    & Willis 2001; Ward et al. 2000) , also confounding generalities about spawning patterns. The

93    species composition of reefs changes as environmental conditions vary, further influencing the

94    patterns of reproduction at the reef scale.  Clearly there is significant scope for reproduction of

95    coral assemblages on reefs to vary regionally and depart from the 'mass spawning' discovered on

96    the Great Barrier Reef (Babcock et al. 1986; Harrison et al. 1984) and subsequently pursued by

97    some investigations of coral reproduction around the world. This variation in timing and

98    synchrony results in a range of reproductive patterns, from temporal isolation of spawning

99    species to a highly synchronous mass-spawning.

100    Mass spawning in scleractinian corals was first discovered on parts of the GBR in austral spring

101    (Harrison et al. 1984; Willis et al. 1985), where it is perhaps more synchronous than on any other

102    coral reef worldwide. However, even on the GBR there is a spatial and temporal variation in

103    mass-spawning. For example, the near-shore reefs spawn one month earlier than those on mid-

104    and outer-shelf reefs (Willis et al. 1985), while the high- and low-latitude reefs have a more

105    protracted period of spawning at times other than during spring (Baird et al. 2009; Baird et al.

106    2002; Harrison 2008; Oliver et al. 1988; Wilson & Harrison 2003). Additionally, spawning times

107    within coral assemblages also vary among years according to the timing of the full moon within

108    the spawning window. The date of the full moon occurs several days earlier each month than in

109    the previous year, causing spawning times to shift periodically (e.g. from October to November)

110    if gametes are not yet mature at the time of full moon. Similarly, when the full moon falls near

111    the edge of the spawning window then only some colonies will have mature gametes, so

112    spawning occurs following two consecutive full moons (e.g. October and November). This

113    phenomenon has been termed 'split spawning' and typically occurs every few years, but can

114    occasionally occur over consecutive years (Baird et al. 2009; Willis 1985).

115    Many of the early studies leading to the discovery of mass spawning on the GBR involved

116    rigorous sampling of colonies using a range of methods throughout the year, which established

117    synchronous reproductive cycles within and among populations (Wallace 1985). This led to

118    more intensive sampling over weeks and days, which established the remarkable synchrony

119    among many colonies and species over a few nights each year. In contrast, some subsequent

120   studies have focused on identifying the species participating in mass spawning events but not

121   quantifying the proportion of participating colonies or the frequency of spawning during other

122   times (nights, weeks, months, and seasons) of the year. Without estimates of the reproductive

123   state of colonies during other times of the year, a relative assessment of the participation in mass

124   spawning events is not possible; if there is a low participation in the mass spawning then there is

125   no knowledge of the other time(s) of spawning, whereas if there is a moderate to high

126   participation then it may be assumed incorrectly that spawning during the other time(s) is

127   negligible. For example, a rigorous sampling of the reproductive state of coral populations

128   throughout the year has identified a second spawning by populations and even some colonies on

129   the GBR (Stobart et al. 1992; Wolstenholme 2004) and other reefs around the world (Dai et al.

130   2000; Guest et al. 2005b; Mangubhai 2009; Mangubhai & Harrison 2006; Oliver et al. 1988).

131   Focussing only on the participation of corals in the mass spawning can also miss the times of

132   reproduction for entire species that are common and functionally important, such as the massive

133   *Porites* (Harriott 1983a; Kojis & Quinn 1982). Additionally, brooding corals are a significant

134   component of many reefs, and planulation in populations and colonies is typically spread over

135   several months throughout the year (Ayre & Resing 1986; Harriott 1992; Harrison et al. 1990;

136   Harrison 2011; Tanner 1996).

137   Despite considerable research effort on the GBR, there is still not a detailed understanding of

138   spatial and temporal variation in coral reproduction at the scale of entire assemblages. This

139   highlights the difficulty in obtaining a similar understanding for the remote coral reefs on

140   Australia's west coast, where far less research has been conducted. Most studies of coral

141   reproduction in Western Australia (WA) have been conducted over a few months at several

142   reefs, of which there are few published accounts (but see Supplementary Table 1), leaving large

143   gaps in knowledge. The gaps are significant because the existing data illustrate the unique

144   patterns of reproduction displayed by WA coral communities and the extent to which they vary

145   among habitats and regions. The rapid industrial expansion through regions of WA in the last

146   decade has seen an increase in the number of studies of coral reproduction, but much of the

147   associated data are contained within confidential reports to industry and government. Here we

148   combine some of the information in this grey-literature with that in public reports and papers, to

149   update our current knowledge of coral reproduction in WA. This includes data for tens of

150   thousands of corals and hundreds of species, from over a dozen reefs spanning 20 degrees of

151  latitude. From these data we identify broad latitudinal patterns, but many gaps in knowledge

152  remain due to paucity of data, biased sampling, and in some instances poor application of

153  methodology. We therefore conclude with a brief discussion around issues of sampling design

154  and methodology, and suggest one approach to quantifying the significance of periods of

155  reproductive output by coral communities, which is among the suite of information required by

156  managers to moderate the effects of human activities along Australia's west coast.

157

158  METHODS

159  **Western Australian regions and sources of reproductive data**

160  Western Australia's coral reefs span more than 12,000 km of coastline and 20° of latitude,

161  ranging from tropical to temperate climates, from coastal reefs to oceanic atolls hundreds of

162  kilometres from the mainland (Veron & Marsh 1988; Wilson 2013). Consequently, WA has a

163  phenomenal diversity of habitats and coral communities, with a corresponding range in reef-

164  level patterns of coral reproduction. Because of these broad patterns in coral community

165  composition, the examination of patterns of reproduction presented here is divided among six

166  regions: (1) Kimberley Oceanic, (2) Kimberley, (3) Pilbara, (4) Ningaloo, (5) Abrolhos and

167  Shark Bay, and (6) Rottnest and southwest WA (Figure 1). Among these regions, the diversity of

168  coral species and genera decreases with increasing latitude (Figure 1), although coral cover can

169  be similar among the tropical reefs and those at the subtropical Abrolhos Islands, before then

170  decreasing in the temperate southwest (Abdo et al. 2012; Johannes et al. 1983; McKinney 2009;

171  Richards & Rosser 2012; Richards et al. 2014; Speed et al. 2013; Veron & Marsh 1988).

172  Regional data or data summaries of coral reproduction were taken from journal articles and

173  public reports, unpublished data, and confidential reports to industry and government

174  (Supplementary Table 1). Where possible, raw data were interrogated and summaries produced

175  across reefs for each region. However, in other instances raw data were not available and

176  regional summaries were based on tables and text within reports that had not been peer-

177  reviewed. Given the scope of these data, discrepancies also existed among studies and there are

178  likely errors in data collection, analyses and species identification. Some regional summaries

179  were adjusted to account for obvious errors in data or conclusions in some reports and the most

180   likely patterns of reproduction were sometimes extrapolated from limited data. Additionally,

181   samples were typically biased by factors such as the environmental conditions, the community

182   composition, the sampling design and the methods used. For example, inferences about the

183   patterns of reproduction on a reef were heavily biased when: data exist for a few species of

184   *Acropora* but the community was dominated by non-*Acropora* corals that reproduce at different

185   times; environmental stress inhibited gametogenesis causing a large portion of the assemblage

186   not to reproduce in a period; spawning was split over two consecutive months but only one

187   month was sampled; coral species and/or genera were incorrectly identified. The issues were

188   most acute in studies with limited spatial and temporal replication. For these reasons, a summary

189   of information that commonly biases inferences about patterns of coral reproduction is presented

190   for each region, to place in context the reproductive data, and times of spawning for species were

191   assigned a level of confidence according to the available data (Table 1, Table 2, and

192   Supplementary Table 2).

193   Coral reef habitats of WA are characterised by widely contrasting environments, but all are

194   exposed to considerable wave energy generated by seasonal cyclones and/or storms.  Reef

195   habitats range from open ocean atolls surrounded by deep oligotrophic waters in the Kimberley

196   Oceanic Region, to reefs heavily influenced by coastal processes such as tidally driven sediment

197   resuspension in the inshore Kimberley and Pilbara Regions.  From the coastal fringing reefs of

198   Ningaloo, to the subtropical and temperate reefs at the Abrolhos Island and the Southwest

199   Region, tidal processes are less extreme, waters are clearer and often lower in nutrients.  This is

200   due in part to the southward flowing Leeuwin Current which intensifies in winter, moderating

201   winter temperature minima and assisting the transport of coral larvae to southern reefs

202   (Cresswell 1996; D'Adamo et al. 2009; Hatcher 1991).  Consequently, there is a high level of

203   reef development in the sub-tropical reefs at the Abrolhos Islands. While the low latitude reefs in

204   the Kimberley have the highest species diversity, they also experience the most pronounced

205   differences in environmental conditions and community composition between the oceanic reefs

206   and those adjacent to the mainland (Richards et al. 2015; Richards et al. 2014). Similarly, within

207   the Pilbara Region, community composition differs between the most frequently studied inshore

208   reefs in the Dampier Archipelago where most reproductive data exist, and mid-shelf around

209   Barrow and Montebello islands (Richards & Rosser 2012; Richards et al. 2014). More

210   information about the environmental characteristics and the context for reef development and

211    coral reproduction in each region is provided in the Supplementary text. Preceding the

212    reproductive summary for reefs within each region is information to place these data in context,

213    which includes: the species diversity and community composition of corals; the number and

214    types of reefs, sites and species for which reproductive data were collected and the time(s) of

215    sampling; whether colonies were affected by disturbances at the times of sampling; and the

216    methods used to infer the times of spawning or planulae release.

217

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.

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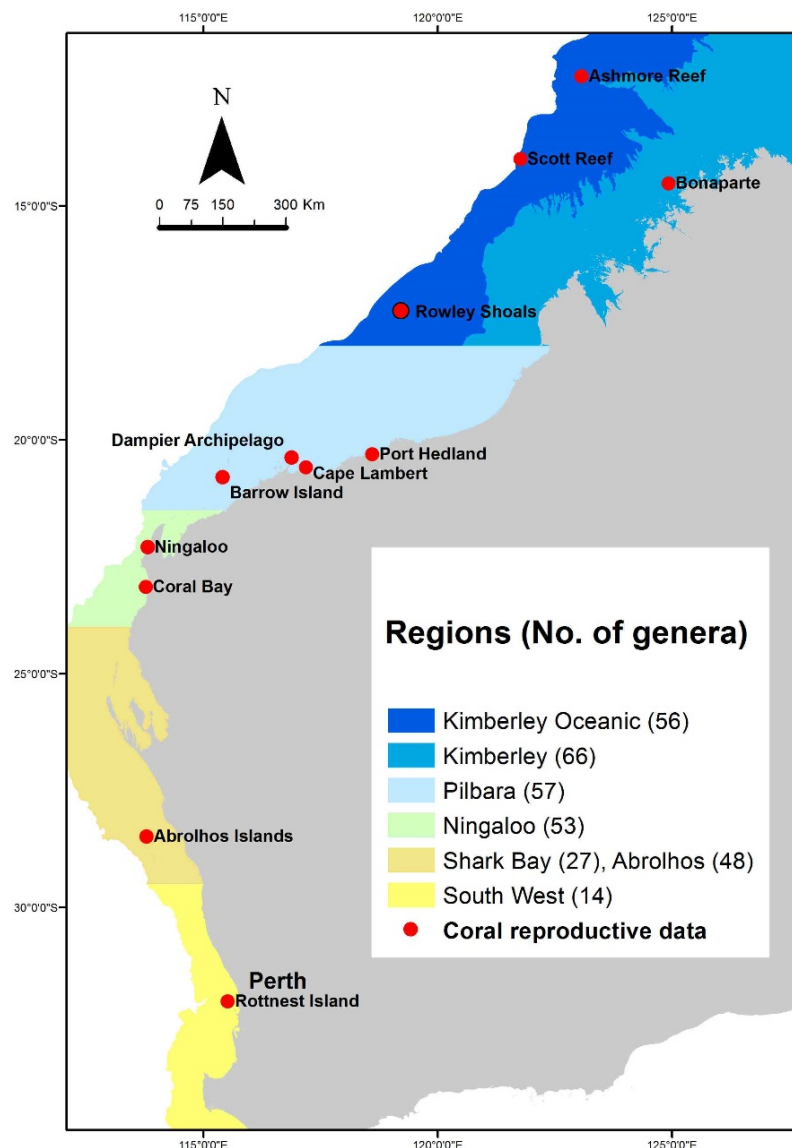


Table 1. Regional variation in coral diversity and reproduction across Western Australia. The number of species within each coral genus know to occur within each region of WA, and the number for which reproductive data are available. The percentage of species within each genus known to reproduce in spring or autumn within each region, of the total sampled. Regions are colour coded according to Figure 1. 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 et al. 2014; Veron 1993; Veron & Marsh 1988).

| Region | Genus | Total known species | Number of species sampled | | Spawning % (number) of species | |
|---|---|---|---|---|---|---|
| | | | Spring | Autumn | Spring | Autumn |
| Kimberley Oceanic | Acropora | 63 | 39 | 49 | 90 (35) | 94 (46) |
| | Echinophyllia | 3 | 1 | 2 | 0 (0) | 100 (2) |
| | Favia | 13 | 4 | 6 | 75 (3) | 100 (6) |
| | Favites | 8 | 3 | 3 | 33 (1) | 100 (3) |
| | Goniastrea | 6 | 2 | 6 | 100 (2) | 100 (6) |
| | Hydnophora | 4 | 2 | 1 | 50 (1) | 100 (1) |
| | Lobophyllia | 3 | 1 | 0 | 100 (1) | - |
| | Merulina | 2 | 2 | 2 | 0 (0) | 100 (2) |
| | Montipora | 28 | 0 | 0 | - | - |
| | Platygyra | 6 | 0 | 3 | - | 100 (3) |
| Kimberley | Acropora | 39 | 35 | 16 | 42 (15) | 87 (14) |
| | Echinophyllia | 3 | 0 | 0 | - | - |
| | Favia | 9 | 2 | 1 | 0 (0) | 100 (1) |
| | Favites | 6 | 2 | 1 | 0 (0) | 100 (1) |
| | Goniastrea | 7 | 4 | 1 | 0 (0) | 100 (1) |
| | Hydnophora | 4 | 4 | 0 | 75 (3) | - |
| | Lobophyllia | 2 | 2 | 0 | 0 (0) | - |
| | Merulina | 1 | 1 | 0 | 0 (0) | - |
| | Montipora | 23 | 0 | 0 | - | - |
| | Platygyra | 5 | 3 | 1 | 0 (0) | 100 (1) |
| Pilbara | Acropora | 49 | 35 | 43 | 34 (12) | 98 (42) |
| | Echinophyllia | 2 | 0 | 0 | - | - |
| | Favia | 10 | 1 | 8 | 0 (0) | 87 (7) |
| | Favites | 7 | 2 | 4 | 50 (1) | 100 (4) |
| | Goniastrea | 7 | 5 | 7 | 0 (0) | 100 (7) |
| | Hydnophora | 4 | 1 | 1 | 0 (0) | 100 (1) |
| | Lobophyllia | 3 | 1 | 2 | 0 (0) | 100 (2) |
| | Merulina | 2 | 1 | 1 | 0 (0) | 100 (1) |
| | Montipora | 28 | 4 | 3 | 0 (0) | 66 (2) |
| | Platygyra | 6 | 4 | 6 | 0 (0) | 100 (6) |
| Ningaloo | Acropora | 41 | 17 | 26 | 12(2) | 92 (24) |
| | Echinophyllia | 2 | 2 | 2 | 0 (0) | 100 (2) |
| | Favia | 8 | 0 | 2 | - | 100 (2) |
| | Favites | 8 | 0 | 1 | - | 100 (1) |
| | Goniastrea | 7 | 1 | 1 | 0 (0) | 100 (1) |
| | Hydnophora | 4 | 1 | 1 | 0 (0) | 100 (1) |
| | Lobophyllia | 4 | 1 | 1 | 0 (0) | 100 (1) |
| | Merulina | 2 | 2 | 2 | 0 (0) | 100 (2) |
| | Montipora | 28 | 2 | 2 | 0 (0) | 100 (2) |
| | Platygyra | 6 | 1 | 2 | 0 (0) | 100 (2) |
| Abrolhos | Acropora | 41 | 0 | 20 | - | 100 (20) |
| | Echinophyllia | 2 | 0 | 1 | - | 100 (1) |
| | Favia | 8 | 0 | 5 | - | 100 (5) |
| | Favites | 8 | 0 | 5 | - | 100 (5) |
| | Goniastrea | 7 | 0 | 2 | - | 0 (0) |
| | Hydnophora | 2 | 0 | 0 | - | - |
| | Lobophyllia | 3 | 0 | 1 | - | 100 (1) |
| | Merulina | 1 | 0 | 1 | - | 100 (1) |
| | Montipora | 26 | 0 | 4 | - | 100 (4) |
| | Platygyra | 2 | 0 | 1 | - | 100 (1) |
| South West | Acropora | 1 | 0 | 1 | - | 100(1) |
| | Echinophyllia | 0 | 0 | 0 | - | - |
| | Favia | 1 | 0 | 0 | - | - |
| | Favites | 4 | 0 | 0 | - | - |
| | Goniastrea | 2 | 0 | 2 | - | 50 (1) |
| | Hydnophora | 0 | 0 | 0 | - | - |
| | Lobophyllia | 0 | 0 | 0 | - | - |
| | Merulina | 0 | 0 | 0 | - | - |
| | Montipora | 1 | 0 | 1 | - | 100 (1) |
| | Platygyra | 0 | 0 | 0 | - | - |

219

220

221    RESULTS

222

223    **Regional patterns of coral reproduction: Kimberley Oceanic**

224    The oceanic reefs of the Kimberley are atolls rising from depths of several hundred meters, with

225    over 300 species and 57 genera of hard corals. Coral cover in many habitats can be over 70%,

226    and much of the remaining substrata are covered in coralline and turf algae, with a very low

227    cover of macroalgae and other benthic organisms. The Acroporidae are typically the dominant

228    family of hard corals, followed by the Poritidae, Faviidae and Pocilloporidae, while soft corals

229    are also common.

230    Coral reproduction has been investigated at all of the Kimberley oceanic reefs during one or

231    more years (Supplementary Table 1). From Ashmore, Cartier, Scott and Seringapatam Reefs, and

232    the Rowley Shoals, several thousand colonies from over 130 species and 30 genera have been

233    sampled during the autumn and/or spring spawning seasons, in one or more years. Of the total

234    number of *Acropora* species know in the region, approximately 62% were sampled in spring and

235    78% in autumn, compared to 20% and 32% of non-*Acropora* species, respectively (Table 1). The

236    majority of the sampling has been conducted at Scott Reef, where there was sampling of colonies

237    prior to the spawning in autumn and spring in consecutive years from 2007 to 2010, including

238    repeated sampling of some tagged colonies. There has been comparatively little sampling at

239    other times of year, so inferences about spawning during summer months may be

240    underestimated. In most instances, the times of spawning were inferred from *in situ* ranking of

241    gamete development, in addition to microscopic investigation of egg sizes and histological

242    analyses of some spawning corals and brooding corals. Spawning has also been observed *in situ*

243    on several occasions.

244    The existing data suggest that most species of corals on the oceanic atolls are broadcast

245    spawners. Spawning has been inferred to occur primarily during spring and autumn, with a larger

246    proportion of species and colonies participating in the autumn mass spawning than in the multi-

247    specific spawning during spring (Table 2; Supplementary Table 2). Many species participated in

248    both spawning events, but most colonies spawn only once a year (i.e. within-population biannual

249    spawning). Of the species of *Acropora* sampled in spring (*n*=39) and autumn (*n*=49), 90% were

250    reproductively active in spring and 94% in autumn, compared to 10% in spring and 32% in

251   autumn for the common non-*Acropora* species (*n*=73) (Table 2; Supplementary Table 2). For the

252   species sampled repeatedly over several years, approximately 40% spawned only in autumn, less

253   than 10% only in spring, and approximately 55% in both autumn and spring; within species, a

254   similar proportion (>30%) of colonies spawning during each season. A similar pattern was

255   evident in the additional 30 species of *Acropora* and 20 species of non-*Acropora* sampled less

256   rigorously (n = 5-10 colonies yr⁻¹), but for a higher proportion of non-*Acropora* species and

257   colonies spawning in autumn; *Favia stelligera* and *F. pallida* spawned during both seasons and

258   *Diploastrea heliopora* spawned only during spring (Supplementary Table 2). More intensive

259   sampling of the non-*Acropora* species may increase the proportion of instances of within-species

260   biannual spawning among these species.

261   Within each season, spawning most commonly occurred during March and October, but varied

262   according to the timing of the full moon. Split-spawning occurred every few years during both

263   seasons and occasionally over consecutive years; splits usually occurring between March and

264   April in autumn, and October and November in spring, following full moons that fell in the last

265   week or so of the preceding months. Spawning has been observed directly in autumn and/or

266   spring during six years, and colonies were sampled before and after to check for the

267   disappearance of pigmented eggs. Based on these observations, spawning usually occurred 7-9

268   nights after the full moon during neap tides. However, the times of spawning varied among years

269   and occurred any time from the night of the full moon to around 10 days after.

270   The majority of corals showed evidence of spawning either in March and/or April, and October

271   and/or November, with the exception of the massive *Porites*. At the times of sampling during

272   autumn and spring, pigmented eggs were observed in only a few massive *Porites* colonies, but

273   massive *Porites* can spawn eggs with comparatively little pigmentation (Stoddart et al. 2012).

274   Histological analyses of samples collected at these times indicated that colonies were dioecious

275   and released eggs and sperm over several months in the year from spring to autumn. A peak in

276   reproductive activity was not obvious, and stages of gamete development indicated spawning

277   over several months from October to May, in contrast to the peak in spawning observed in

278   massive *Porites* on other reefs around Australia (Kojis & Quinn 1982; Stoddart et al. 2012). The

279   sampling of all species was restricted a few months each year around two main spawning events,

280   and the extent of spawning following other lunar phases and months has not been investigated in

281   detail. The potential exists for at least some colonies and/or species to spawn during other times.

282   For example, a small proportion of *Acropora millepora, A. tenuis, A. polystoma, A. gemmifera*

283   and *Goniastrea edwardsii* colonies at Ashmore Reef had pigmented eggs in early February or

284   September 2011, indicating they would either spawn a month earlier than most other corals or

285   would retain their eggs until the next month; alternately, early spawning in some corals during

286   2011 could reflect higher than normal water temperatures. In addition the variation in times of

287   broadcast spawning, larval production in the brooding corals also occurs outside of the dominant

288   spawning events. Histological analyses confirmed that *Isopora brueggemanni, I. palifera,*

289   *Seriatopora hystrix* and *Stylophora pistillata* were brooding corals in the offshore Kimberley

290   region. *Isopora brueggemanni* and *S. hystrix* were most intensively sampled and contained

291   gametes in all stages of development and planula larvae during most months from October to

292   May. There was no clear peak in reproductive activity in the brooding corals and larvae were

293   apparently released over many months from spring to autumn.

294

295   **Regional patterns of coral reproduction: Kimberley**

296   There are diverse and extensive reef systems throughout Kimberley region, including inner shelf,

297   fringing and patch reefs, exposed platforms and subtidal banks around the coastline and islands

298   (Richards et al. 2014; Speed et al. 2013; Wilson 2013).  There are over 300 species of hard corals

299   from 71 genera, and clear cross-shelf differences in species distributions exist between the

300   coastal and offshore locations, with 27 species (8%) recorded only from nearshore locations and

301   111 species (33%) recorded only at offshore locations (Richards et al. 2014). There are no

302   quantitative data describing the relative abundances of corals throughout the inshore Kimberley,

303   but qualitative descriptions highlight the considerable variation in habitats and coral

304   assemblages. For example, leeward intertidal reefs may be characterised by branching and

305   tabular *Acropora*; subtidal zones can have a high cover and diversity of corals dominated by

306   massive *Porites* and species of Faviidae and foliose corals; exposed fringing reefs may have a

307   comparatively low cover and diversity of corals dominated by massive Faviidae and soft corals;

308   extensive tidal pools throughout the region can have a high cover and diversity of corals different

309   to those in other zones (INPEX 2011; Wilson 2013) .

310    There are very few reproductive data for coral assemblages in the inshore Kimberley region,

311    particularly given the extent and diversity of the reefs (Supplementary Table 1). Inferences of

312    coral reproduction in the region are largely based on surveys during one or two years at a small

313    group of islands within the Bonaparte Archipelago (Figure 1). Several hundred colonies from

314    around 60 species and 15 genera were sampled during autumn or spring season, with sampling

315    focusing on species of *Acropora* (Table 1; Supplementary Table 2). Of the total number of

316    *Acropora* species know in the region, approximately 90% were sampled in spring and 40% in

317    autumn, compared to 30% and 4% of non-*Acropora* species, respectively. Inferences about

318    spawning during these seasons were drawn from *in situ* or microscopic examination of

319    pigmented eggs within colonies, and there are no observations of coral spawning for the inshore

320    Kimberley reefs.

321    The main season of spawning on inshore Kimberley reefs is probably during autumn, but with

322    second multi-specific spawning also occurring during spring at a similar time to the oceanic reefs

323    in the region (Table 2; Supplementary Table 2). Of the species of *Acropora* sampled in spring

324    (*n*=35) and autumn (*n*=16), 42% were inferred to spawn in spring and 87% in autumn (Table 2).

325    Of the 60 common non-*Acropora* species, there was evidence of only 5% spawning in spring and

326    7% in autumn. The low proportion of non-*Acropora* spawning at these times suggests

327    reproductive activity outside the peak spring and autumn spawning windows by these taxa,

328    and/or is a consequence of low replication and a possible split-spawning. Although not observed

329    *in situ*, spawning by a few species of Mussidae and Faviidae in aquaria at Kimberley Marine

330    Research Station (KMRS) at Cygnet Bay occurred at a similar time as at the oceanic reefs during

331    two years, 7-9 nights after full moon in March (A. McCarthy & A. Heyward, pers. comm.).

332    There is currently no evidence of spawning in the inshore reefs of the Kimberley occurring a

333    month earlier than on the oceanic reefs, as tends to occur on parts of the Great Barrier Reef. If

334    this was to occur in the Kimberley, spawning on the inshore reefs would be expected in February

335    or March in autumn, and September or October in spring. Although sampling has not been

336    conducted during these months, the existing data demonstrate that spawning did not occur

337    exclusively a month earlier than on the oceanic reefs and that multi-specific spawning events

338    have also occurred later in the season, during April in autumn and November in spring. Evidence

339    for late spawning during autumn and spring may reflect a split-spawning during the years of

340    sampling, as on the oceanic reefs.

341 Of 31 species sampled from seven genera on the inshore Kimberley reefs during late March, 30
342 had pigmented eggs and were likely to spawn in early April. This included many species that
343 were sampled with low ($\leq 5$ colonies) replication, indicating that autumn is the main season of
344 spawning. Indeed, based on the timing of the full moon and spawning on the oceanic reefs, the
345 autumn spawning during that that year (2007) was likely spilt; so many colonies and species may
346 have also spawned in early March, providing further evidence for autumn being the primary
347 season of spawning for the region. Of 63 species sampled in late October, 25% contained
348 pigmented eggs and were likely to spawn in early November, of which the majority were
349 *Acropora*; 37% of the 35 species of *Acropora* contained pigmented eggs. However, eggs were
350 absent from many of the colonies sampled with low replication ($\leq 5$ colonies) and the spring
351 spawning may have been split, based on the timing of the full moon and the data for the oceanic
352 reefs. Consequently, a proportion of colonies and species probably spawned in early October and
353 future work may identify a higher proportion of species and colonies participating in a spring
354 spawning. It remains to be determined whether the inshore reefs of the Kimberley display a
355 similar degree of spawning synchrony during any one month in autumn and spring as on the
356 oceanic reefs, or whether inshore spawning is more protracted over several months with seasonal
357 peaks around autumn and spring, as may be the case on Indonesian reefs to the north (Baird et al.
358 2009). There are few data for the non-*Acropora* corals, which are most likely to have less
359 synchronous patterns of spawning, and nor are there currently any data for brooding corals that
360 are probably common throughout parts of the region. The brooding corals in the Kimberley are
361 likely to display similar patterns of reproduction to those at the oceanic reefs, with planulation
362 occurring during many months through spring to autumn, and perhaps extending into some
363 winter months.

364

**Regional patterns of coral reproduction: Pilbara**
365
366 There are extensive near-shore and mid-shore reefs systems throughout the Pilbara. Within the
367 region much of the available information exists for the Damiper Archipelago (e.g. Blakeway &
368 Radford 2004; Griffith 2004; Marsh 2000; Richards & Rosser 2012; Veron & Marsh 1988) and
369 there is less information for reefs in the west Pilbara (but see Marsh 2000; Richards & Rosser
370 2012; Veron & Marsh 1988). The general pattern of coral diversity is similar throughout the

371   Pilbara, with between 200 and 230 species recorded at the Dampier Archipelago, and at the mid-

372   shore Montebello and Barrow Island reefs. A slightly higher number recorded at the Dampier

373   Archipelago may be due to greater diversity of habitats and environmental conditions (Griffith

374   2004; Marsh 2000; Richards & Rosser 2012). However, there are distinct assemblages of coral

375   species among the inshore reefs and those throughout the archipelago, reflecting the cross-shelf

376   variation in environmental conditions and habitat types (Blakeway & Radford 2004; Richards &

377   Rosser 2012). Average total hard coral cover for the inshore reefs of the Pilbara is approximately

378   20%, with the dominant families Faviidae and Dendrophylliidae having contributed to much of

379   this cover (Speed et al. 2013). However, coral community composition can also vary

380   dramatically among the inshore reefs and species of *Acropora*,  Faviidae, *Platygyra*, *Turbinaria*

381   and *Pavona* are common in some communities (Blakeway & Radford 2004). The outer reefs of

382   the west Pilbara can have communities characteristic of clearer water, with approximately twice

383   the coral cover and a higher diversity. In particular, within the back-reef habitats many massive

384   *Porites* colonies are associated with extensive coral assemblages, including a high cover (>50%)

385   of *Acropora* (Marsh 2000; Speed et al. 2013).

386    Coral reproduction in the Pilbara region has been investigated at several reefs, with over 1000

387   colonies sampled from 115 species, during one or more years (Supplementary Table 1). Of the

388   total number of *Acropora* species know in the region, 71% and 88% were sampled in spring and

389   autumn, respectively, compared to 28% and 46% for the non-*Acropora* species (Table 1;

390   Supplementary Table 2). By far the majority of these data were from the Dampier Archipelago,

391   and the times of reproduction were inferred from *in situ* ranking of gamete development,

392   microscopic investigation of egg sizes and histological analyses of some spawning and brooding

393   corals. Spawning has also been observed *in situ* on several occasions. Given the frequency and

394   timing of disturbances to Pilbara reefs in recent years, including dredging operations,

395   temperature anomalies and cyclones, some data from the region were probably biased by coral

396   colonies having insufficient energy reserves to invest in reproduction. In these instances, the

397   proportion of species and colonies reproducing could be underestimated.

398   The first discovery of coral spawning in Western Australia was in the Dampier Archipelago

399   (Simpson 1985). Early research showed corals spawning exclusively in autumn over two

400   consecutive years, in 46 species of coral from seven families. The presence of mature eggs in

401   some non-*Acropora* species after the main spawning event indicated split-spawning over two

402    consecutive lunar cycles, but there was no evidence of spawning during spring. Subsequent

403    research has documented multi-specific spawning by a small proportion of colonies and species

404    during spring (October to December). Within the Dampier Archipelago, a small number of

405    tagged colonies seemed to spawn consistently either in autumn or in spring and have only one

406    gametogentic cycle. Of the species of *Acropora* sampled in spring ($n$=35) and autumn ($n$=43),

407    34% were inferred to spawn in spring and 98% in autumn (Table 2; Supplementary Table 2). Of

408    the 69 common non-*Acropora* species, 43% spawned in autumn and one spawned in spring,

409    although few were sampled in spring. Among the non-*Acropora* species, only *Favites flexuosa,*

410    and possibly *Favites pentagona* and *Montipora undata* are thought to spawn in spring or early

411    summer, while the proportion of colonies within species of *Acropora* known to spawn during

412    spring is generally low (< 20%) (Table 2; Supplementary Table 2). Sampling around a split-

413    spawning and with environmental stress has potentially underestimated the participation by

414    corals in the spring spawning (October to December), but the primary spawning period is

415    certainly autumn (usually March).

416    Many Pilbara reefs are dominated by corals such as massive *Porites*, *Pavona decussata* and

417    *Turbinaria mesenterina*, which display different patterns of reproduction to most hermaphroditic

418    species that participate exclusively in the spring and/or autumn spawning events. Within the

419    Dampier Archipelago, repeated histological examination showed that these three taxa were

420    gonochoric. Spawning occurred predominantly in December in the massive *Porites* (mainly *P.*

421    *lobata*), as on the Great Barrier Reef (Harriott 1983). For *Pavona decussata,* spawning occurred

422    during March and April, possibly due to split-spawning during that year (2007). In *Turbinaria*

423    *mesenterina*, spawning occurred over several months, possibly from November to April. While

424    *T. mesenterina* retained eggs after this period, this does not indicate imminent spawning as this

425    species has been reported to have a gametogenic cycle of more than 12 months (Willis 1987).

426    While spawning has not been observed, frequent sampling of *P. lutea* demonstrated that it

427    spawned during spring tides predominantly 3 days (2-4 days) after the full moon, in contrast to

428    the usual times of spawning during neap tides approximately one week after the full moon. In

429    addition to these spawning corals, the main periods of reproductive output for the brooding

430    corals in the Pilbara are also likely to occur at times other than during the dominant spawning

431    periods in autumn and spring. Although cycles of gametogenesis in brooding corals have not yet

432   been investigated in the Pilbara, they probably culminate in the release of planula larvae over

433   several months through spring to autumn, and possibly into winter months.

434

**Regional patterns of coral reproduction: Ningaloo**

436   Ningaloo is an extensive fringing reef system almost 300 km in length, with diverse coral

437   communities and over 200 species of hard corals from 54 genera (Veron & Marsh 1988). Mean

438   coral cover can be as high as 70% at areas of the reef flat and reef slope, but is typically less at

439   other habitats such as in the lagoon (Speed et al. 2013). The remaining benthic cover is

440   composed of coralline and turf algae, seasonal macroalgae growth and other benthic organisms.

441   Within the coral communities, the Acroporidae are often most abundant, but the Faviidae,

442   Poritidae, Pocilloporidae and soft corals are also common (Speed et al. 2013; Veron & Marsh

443   1988). The deeper lagoons typically contain massive *Porites* bommies and patches of staghorn

444   *Acropora* , while the outer-slope is dominated by robust corals with massive and encrusting

445   growth forms, often *Platygyra sinensis* and prostrate *Acropora* (Wilson 2013).

446   There is detailed reproductive data for some species at one location at Ningaloo and a

447   comparatively poor understanding of spatial variation across this extensive system

448   (Supplementary Table 1). Coral reproduction has been investigated during several years, for

449   several hundred colonies from 42 species and 11 genera (Table 1). Of the total number of

450   *Acropora* species know in the region, approximately 44% were sampled in spring and 67% in

451   autumn, compared to 14% and 20% of non-*Acropora* species, respectively. Most data exist for

452   several species of Acroporidae and Faviidae sampled during one or more months from spring to

453   autumn at Coral Bay. Early work at Ningaloo suggests some variation in the time of spawning

454   may exist among locations, with a higher proportion of corals spawning in March in the north

455   and in April to the south, but this may also have been a consequence of split-spawning.

456   Nonetheless, the studies of coral spawning at Coral Bay provide detailed information about

457   temporal variation in spawning among months, lunar cycles, and the nights of spawning in

458   autumn. Inferences about spawning times were drawn from *in situ* ranks of gamete development

459   and microscopic investigation of egg sizes in random population samples and by re-sampling

460   individual colonies, in addition to direct observations of spawning *in situ*.

461     Mass spawning at Ningaloo occurs during autumn, with a more protracted period of spawning

462     over consecutive months, and little or no multi-specific spawning during spring (Table 2;

463     Supplementary Table 2). Of the species of *Acropora* sampled in spring ($n$=17) and autumn

464     ($n$=26), 12% were inferred to spawn in spring and 92% in autumn, with one spawning

465     exclusively in summer. Of the 69 common non-*Acropora* species, none were reproductively

466     active in spring, compared to 20% in autumn (Table 2; Supplementary Table 2). However, a low

467     proportion of species (< 20%) and particularly colonies have been sampled during spring.

468     Additionally, there are very few reproductive data from parts of Ningaloo other than Coral Bay.

469     Most Acroporidae and Faviidae colonies at Coral Bay participated in mass spawning during a

470     single month in autumn, but a small proportion of many species also spawned during other

471     months through summer and autumn. Species typically spawned during one or two consecutive

472     months, with no evidence of spawning during discrete months or of a multi-specific spawning

473     during spring, as on northern reefs. There are numerous observations of slicks of coral spawn

474     during spring, but the extent to which these are a product of multi-specific spawning remains

475     unknown (R Babcock & D Thompson pers. comm.). Within species, individual colonies had a

476     single gametogenic cycle and usually spawned within a few consecutive nights. The mass

477     spawning usually occurred during neap tides in late March or early April, 7-10 nights after the

478     preceding full moon, but a small proportion of colonies of several species also spawned

479     following the full moon or the new moon during months either side of the mass spawning.

480     Within the species spawning during autumn, most of their colonies (60 – 100%) participated in

481     the mass spawning in early April following the full moon in late March, but during other years

482     mass spawning occurred in the last week of March following an earlier full moon in March.

483     Around the quantified mass spawning events in early April, a relatively small (< 20%)

484     proportion of colonies from most species also spawned a month earlier (early March) or later

485     (early May), following the preceding full moon or new moon, particularly in the non-*Acropora*

486     species. A higher proportion (10-20%) of these colonies spawned during March than in May (<

487     10%), which may be due to a split-spawning during the years of sampling or may be typical of a

488     more protracted spawning at Ningaloo. Early observations suggest that split-spawning is a

489     common feature at Ningaloo, but whether it occurs during the same years and involves a similar

490     proportion of species and colonies as on reefs further north remains to be determined. Cooler

491     waters at Ningaloo could result in slower rates of gametogenesis and an increased likelihood of

492   split-spawning during years in which a full moon falls early in March, and/or a higher proportion

493   of colonies participating in an April spawning than on northern reefs.

494   There was little evidence of spawning at Ningaloo during months other than in autumn. Less

495   than a few percent of colonies of *Goniastrea retiformis*, *A. humilis* and *A. papillarae* had visible

496   eggs in October, but none were pigmented and the times of spawning were unknown. Existing

497   data suggests that *A. papillarae* is the only species that does not participate in mass spawning

498   and spawns exclusively during summer, probably during December and/or January.

499   Additionally, a small proportion (<5%) of *Echinopora lamellosa* also spawned during summer in

500   February, but with a higher proportion spawning during March (≈ 13%) and particularly April (≈

501   80%). There are currently no data for species of corals such as massive *Porites* known to spawn

502   during summer at other reefs throughout WA. Given that spawning seems to be more protracted

503   at Ningaloo, future work may identify a higher proportion of species and colonies spawning

504   during summer, particularly for the non-*Acropora*. There is also no existing information for the

505   times of planulation in brooding corals at Ningaloo, but planula release is likely to occur at

506   similar times to other northern reefs, from spring through to autumn, with perhaps a lower

507   incidence in spring due to the cooler water temperatures.

508

509

510   **Regional patterns of coral reproduction: Abrolhos Islands and Shark Bay**

511   The Houtman Abrolhos Islands have the highest latitude coral reefs in Western Australia. The

512   coral communities are scattered among four islands, situated < 100 km from the coastline but

513   near the edge of the continental shelf, with over 180 species from 42 genera of corals (Veron &

514   Marsh 1988). Coral cover ranges between 35 and 85% among habitats (Dinsdale & Smith 2004),

515   with an average cover for the region of approximately 44% (Speed et al. 2013). Unlike studies on

516   a comparable latitude on the east coast of Australia (Harriott & Banks 2002), the Abrolhos

517   maintains high percentages of tabulate and particularly staghorn *Acropora* (Abdo et al. 2012;

518   Dinsdale & Smith 2004). Much of the remaining substrata were covered in turf and coralline

519   algae, although patches of macroalgae are also common. Situated to the north of the Abrolhos

520   Islands, Shark Bay is a large shallow bay (~12,950 km²) with an average depth of 9 m and is

521     enclosed by a number of islands (Veron & Marsh 1988). The bay consists of vast seagrass

522     meadows (Wells et al. 1985) and coral growth is restricted to waters with oceanic salinity, such

523     as in the western side of the bay (Veron & Marsh 1988), where 82 species from 28 genera of

524     hard corals have been recorded (Veron & Marsh 1988). Corals from the families Acroporidae

525     and Dendrophylliidae are found in similar abundance of approximately 10 -15% cover, and other

526     genera found in low (<2%) cover include *Montipora*, *Platygyra*, *Pocillopora*, and *Porites*

527     (Bancroft 2009; Cary 1997; Moore et al. 2011; Speed et al. 2013).

528     Coral reproduction has primarily been investigated during one year at the Abrolhos Islands,

529     around the predicted time of mass spawning in autumn (Supplementary Table 1). Of the total

530     number of species know in the region, approximately 49% of the *Acropora* and 34% of the non-

531     *Acropora* were sampled in autumn, but with no sampling at other times of the year (Table 1).

532     Several hundred colonies from 107 species and 10 families were sampled in March 1987, and a

533     small random sample of colonies during late February 2004 (Supplementary Table 2). Most

534     samples were from species of *Acropora* and Faviidae around the Wallabi group of islands. The

535     times of spawning were inferred from *in situ* ranking of gamete development, microscopic

536     investigation of egg sizes and stages, and direct observation of spawning *in situ* and in aquaria.

537     In addition to random sampling, tagged colonies were re-sampled before and after the main

538     nights of spawning.

539     There is clearly a mass spawning by a high proportion of many *Acropora* species at the Abrolhos

540     Islands during autumn, but no knowledge of whether corals also spawn during spring or summer

541     (Table 2, Supplementary Table 2). Of the 107 species sampled, 58 species participated in the

542     main two nights of spawning in March, with a further 36 species likely to spawn on other nights

543     during March; a similar proportion of *Acropora* (49%) and non-*Acropora* (31%) participated in

544     the March spawning. Spawning occurred primarily over the 10 and 11 nights after the full moon,

545     during spring tides of small amplitude (<2 m), with reports of other spawning events also

546     between 8 and 11 nights after the full moon. In addition to the species and colonies that spawned

547     over a few consecutive nights, there was also evidence of a more protracted spawning by many

548     colonies and species over a greater number of nights, and possibly also during April and/or other

549     seasons. Within the species of mass-spawners, the mean number of colonies participating was

550     70%, and ranged between 10 and 100%. Most species spawned over a few nights, but within the

551     assemblage spawning was probably protracted over almost three weeks, as early as a few nights

552  before the full moon and up to two weeks later. Additionally, gametes were absent from a

553  variable proportion of colonies in approximately half the species observed to spawn in March,

554  and from all colonies in an additional 13 species, suggesting they either did not spawn during

555  that year or were likely to spawn during a different season. Slicks of spawn have also been

556  observed at the Abrolhos in February, although subsequent sampling suggested the bulk of the

557  community was likely to spawn in March. The species known to spawn during months other than

558  March on more northern reefs were either not sampled, or had a proportion of colonies without

559  eggs and were sampled in low replication. There is currently no reproductive information for

560  brooding corals, which are likely to release planulae over several months from spring to autumn,

561  but with perhaps a reduced reproductive window due to cooler water temperatures.

562

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

564  Within the temperate southwest region of WA, corals are near their geographical limit. Reefs

565  where corals are known to occur include Rottnest Island, Hall Bank, and some patches of reef

566  within lagoons adjacent to the Perth mainland, such as at Marmion and Jurien. Rottnest Island

567  has the most abundant coral communities, with 25 species from 16 genera. *Pocillopora*

568  *damicornis* dominates certain areas (Veron & Marsh 1988), which is a consequence of clonal

569  reproduction (Stoddart 1984). Clonal reproduction may also be important for other species at

570  Rottnest Island with more tropical affinities, such as *Acropora* sp. and *Porites lutea* (Crane

571  1999). Among the remaining corals, the dominant taxa are species of Favidiiae with subtropical

572  affinities, such as *Goniastrea australiensis*. Macroalgae (*Sargassum* and *Ecklonia*) are common

573  around Rottnest Island and contribute up to 60% of benthic cover (Wells & Walker 1993).

574  Between Rottnest Island and the Perth metropolitan coastline is Hall Bank, a small reef with a

575  low diversity (14 spp.) but a high cover (≈50%) of corals, of which most are *Favites* and

576  *Goniastrea* (Thomson & Frisch 2010). In contrast, the reefs adjacent to the coastline have a

577  lower coral diversity and cover, such as Marmion lagoon with 10 species from eight genera

578  (Veron & Marsh 1988). Fleshy macroalgae are dominant on most of the temperate reefs, but

579  corals are can often be found among the algae in low density (Thomson et al. 2012). The most

580  abundant coral on these reefs is *Plesiastrea versipora*, one of the Indo Pacific's most widespread

581     corals, however it rarely reaches large sizes and other species tend to have higher cover (e.g.

582     *Goniastrea* spp. *Montipora capricornis*).

583     Throughout the southwest region, coral reproduction has been investigated only at Rottnest

584     Island during one or more years throughout the 1980s and (Supplementary Table 1). At Rottnest

585     Island, a total of nine species and >600 colonies were sampled over multiple seasons, for months

586     to years (Table 1). The majority of the sampling has been conducted at two sites, which includes

587     consecutive sampling and spawning observations of colonies prior to spawning around summer

588     and autumn from January to May. Histological analyses were also used to investigate

589     reproduction in three species (*Pocillopora damicornis, Alveopora fenestrata* and *Porites lutea*)

590     from December to April. Mature gametes were found in colonies of the most abundant spawning

591     corals over several months through summer and autumn (Table 2, Supplementary Table 2).

592     Histological analyses revealed *Pocillopora damicornis* at Rottnest Island to be both a brooding

593     and spawning coral. Gametes and planula larvae were common in colonies through summer to

594     winter (December to early April), being most common in March, and rare or absent in winter.

595     The available data for the southwest region are only from Rottnest Island where spawning by the

596     dominant species appears to occur through summer and or autumn months (e.g. *Goniastrea*

597     *aspera*, *G. australensis*, *Montipora mollis* and *Symphillia wilsoni*), a pattern similar to that seen

598     on the subtropical reefs of Australia's east coast. Some colonies have been observed to spawn

599     around the time of new moon rather than full moon, such as *Symphyllia wilsoni*, and *Alveopora*

600     *fenestsrata*. Among the other dominant coral species in the region, there appears to be an

601     extended reproductive season of two or more months at different times of year for different

602     corals; for example, in summer for *Pocilloproa damicornis*, in early autumn for *Turbinaria*

603     *mesenterina*. The apparent staggering of reproduction among species between February and May

604     suggests that there is a relatively low level of synchrony within the temperate coral communities,

605     but with perhaps a higher degree of synchrony among some conspecific colonies in late summer

606     (Supplementary Table 2). Because the species composition and level of coral cover varies so

607     markedly among coral assemblages in the southwest, there is little or no knowledge of spatial

608     variation in community reproduction throughout the region. For example, *Plesiastrea versipora*

609     is numerically the most common coral in the region and across southern Australia, yet its

610     reproductive biology in temperate waters is still poorly understood. It is recorded as a mass

611     spawner on tropical reefs (Magnetic Island, Babcock et al. 1986; Taiwan, Dai et al. 1992), but

612   did not spawn with other subtropical corals such as *G. australiensis* in Moreton Bay, on the east

613   coast of Australia (Fellagara et al. (2013). There is no knowledge of the distribution and patterns

614   of reproduction in brooding corals through the southwest region, with the exception of

615   *Pocillopora damicornis* at Rottnest Island.

616

617

618   DISCUSSION

619

620   **Summary of coral reproduction across Western Australia**

621   The observed differences in reproduction among Western Australian (WA) coral reefs are due to

622   their varying community composition, modes of reproduction, and the cycles of gametogenesis

623   for coral species. The most obvious differences in community composition are the higher

624   abundance and diversity of Acroporidae and massive *Porites* on offshore reefs and tropical reefs

625   north of the Abrolhos Islands. Among the inshore reefs and those south of the Abrolhos Islands,

626   species of Faviidae, Pocilloporidae, *Turbinaria* and/or *Pavona* are more common and there is a

627   notable decline in the abundance and diversity of coral species (Lough & Barnes 2000; Speed et

628   al. 2013; Veron & Marsh 1988). Beyond the effect of community composition, the modes of

629   reproduction displayed by the different coral species distinguished their cycles of gametogenesis

630   and times of reproductive output.

631   As on most tropical reefs around the world, the dominant mode of coral reproduction on WA

632   coral reefs is broadcast spawning. Within a year, most individual corals have a single cycle of

633   gametogenesis that culminates in spawning during one or a few consecutive nights each year.

634   However, the times of spawning and the degree of synchrony among and within species vary

635   among the different regions, with a latitudinal gradient in the spawning activity among seasons.

636   The primary period of spawning on all WA reefs (apart from the southwest region) is in autumn,

637   often culminating in the mass spawning of a relatively high proportion of species and colonies

638   during March and/or April.

639   Successive studies have added to the list of species known to mass spawn during autumn, but

640   also to the list known to participate in a second multi-specific spawning during spring (October

641   and/or November) on many WA reefs. The existing data suggest that biannual spawning by

642   communities during autumn and spring is a phenomenon that occurs with increasing frequency

643   from Ningaloo Reef north. Although more intensive sampling is necessary to clearly establish a

644   latitudinal gradient, synchronous spawning by multiple species and colonies in the spring

645   spawning is highest on the Kimberley Oceanic reefs, decreases considerably on Pilbara reefs,

646   and may not occur on Ningaloo Reefs – there is only anecdotal evidence of multi-specific

647   spawning at Ningaloo Reef in spring. Of the 17 species of biannual spawners on the Kimberley

648   Oceanic reefs that were sampled most rigorously in the other regions of WA, all spawned in

649   autumn and five during spring in the Pilbara, and all spawned in autumn and none during spring

650   at Ningaloo (Table 2). In addition to the reduction in spring spawning with increasing latitude,

651   spawning may also become more protracted over consecutive nights or weeks around the mass

652   spawning in autumn from reefs in the Kimberley to the Abrolhos Islands (Table 2), although

653   more data are again required to confirm this pattern.

654   Within these seasons, there is a comparatively poor understanding of spatial and temporal

655   variation in spawning times (months, weeks, time of day). Mass spawning occurs most

656   commonly in March and/or April, and the multi-specific spawning in October and/or November,

657   often varying according to the timing of the full moon. As with coral communities on the Great

658   Barrier Reef, spawning on WA reefs can be split over consecutive months in autumn and spring,

659   depending on the timing of the full moon. The phenomenon typically occurs every few years, but

660   can also occur in consecutive years. The nights of spawning were typically inferred from the

661   presence of pigmented eggs in colonies days to weeks before the predicted dates, with very few

662   direct observations of spawning and limited sampling conducted after the event. There is

663   certainly a peak in spawning activity (mass spawning) over a few nights each year on most reefs,

664   but with a variable participation by colonies and species in this primary spawning event. Most

665   commonly, mass spawning occurs during neap tides between approximately 7 to 12 nights after

666   the full moon, usually in March and/or April, on all reefs but for those in the temperate

667   southwest region. However, intensive sampling of colonies over days and weeks at Ningaloo

668   Reef has also documented spawning around the time of the new moon, as can occur in some

669   species on the GBR (Babcock et al. 1986). Whether this pattern reflects a more protracted

670   spawning that is unique to Ningaloo Reef, or is a feature of other WA reefs remains to be

671   determined.

672

Table 2. Regional variation in spawning for coral species sampled most rigorously on Western Australian reefs. 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. Taxonomic revisions are summarised in Supplementary Table 2. 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.

| 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 | | |
| | s | o | n | d | j | f | m | a | m | s | o | n | d | j | f | m | a | m | s | o | n | d | j | f | m | a | m | s | o | n | d | j | f | m | a | m | s | o | n | d | j | f | m | a | m | s | o | n | d | j | f | m | a | m |
| *Acropora aspera* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora cytherea* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora digitifera* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora florida* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora gemmifera* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora humilis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora hyacinthus* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora intermedia* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora latistella* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora microphthalma* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora millepora* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora samoensis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora secale* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora spicifera* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acropora tenuis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Favia pallida* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Favia stelligera* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Favites halicora* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Goniastrea aspera* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Goniastrea australensis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Goniastrea retiformis* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Lobophyllia hemprichii* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Merulina ampliata* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Platygyra daedalea* | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

673

674    Despite some brooding corals being widely distributed and abundant on many of WA's coral

675    reefs (e.g. species of Pocilloporidae and *Isopora*), there is currently little information about their

676    cycles of gametogenesis and times of planulae release. Within a year, brooding corals on WA

677    reefs probably have multiple cycles of gametogenesis culminating in the release of planluae

678    larvae over several months, similar to those on the GBR (Harriott 1983b; Harrison et al. 1990;

679    Kojis 1986; Tanner 1996; Wallace et al. 2007). On the Kimberley Oceanic reefs, planulae were

680    present within *Isopora brueggemanni* and *Seriatopora hystrix* during several months through

681    spring to autumn. Brooding corals on other WA reefs probably have similar cycles of

682    planulation, but for perhaps a shorter reproductive window on higher latitude reefs. The relative

683    proportion of planulae produced during different months of the year and the nights of their

684    release relative to the phases of the moon are unknown for all brooding corals on all reefs.

685

686    **Methods for assessing coral reproduction**

687    Consideration of coral reproduction is often required by environment mangers where

688    development activities are proposed on or near coral reefs. The principle being that if coral

689    spawning and larval settlement are concentrated during a discrete period then the potential

690    impacts from development works can be minimised. Rigorous sampling and interpretation of

691    reproductive status in coral communities is needed well in advance to provide time for planning;

692    sampling is also needed to continue throughout to confirm predictions about time(s) of spawning.

693    In all cases, the accurate prediction of the timing, magnitude and duration of coral spawning is

694    vital given the logistical complexity of development operations and the cost of delays.

695    Many early studies of coral reproduction employed rigorous, and often complimentary, methods

696    because so few data existed. The resulting publications provided a detailed description of the

697    methodology and the assumptions on which conclusions were based. Attempts to quantify cycles

698    of reproduction today require a good knowledge of this background literature, and particularly

699    the limitations of the different approaches. The most relevant literature and methods for a

700    particular study will depend on the questions to be addressed, the regions in which the reefs are

701    found and the species to be investigated. However, to maximise the knowledge gained and

702    minimise the biases from sampling effort, many publications should first be read and understood;

703    some examples include (Alino & Coll 1989; Ayre & Resing 1986; Done & Potts 1992; Fadlallah

704 1983; Fan & Dai 1995; Fong & Glynn 1998; Glynn et al. 1994; Glynn et al. 1991; Harrison

705 1993; Harrison et al. 1990; Heyward & Collins 1985; Sakai 1997; Sebens 1983; Shlesinger et al.

706 1998; Stoddart 1983; Stoddart & Black 1985; Szmant-Froelich et al. 1985; Szmant & Gassman

707 1990; Wallace 1985). In the context of environmental management, we provide some comments

708 on the experimental design and methodology used in coral reproductive studies in Western

709 Australia, which also provides some background to a thorough reading of the existing literature.

710

711 **Community composition:** For environmental management, information about coral

712 reproduction is often required at the level of the entire community. Thus, there is a need to assess

713 the composition of coral communities across the susceptible reefs, habitats and sites, in order to

714 quantify the relative dominance of the species. As the species list of corals at tropical reefs can

715 be extensive, a convenient cut-off point must be chosen. Therefore, we suggest that the species

716 be ranked in terms of their contribution to total coral cover, and those making a cumulative

717 contribution to most (≈80%) cover across all communities of interest be chosen for assessment of

718 reproductive behaviour. However, consideration must also be given to whether certain species,

719 although low in relative abundance, play a critical role in ecosystem maintenance (e.g. keystone

720 species).

721

722 **Taxonomic resolution:** Coral taxonomy and the identification of species for sampling are

723 problematic in virtually any study of tropical coral communities; the issue cannot be understated.

724 Identification to the finest taxonomic resolution possible is always desirable, however the

725 suggested approach of quantifying seasonal reproductive patterns for dominant taxa would work

726 equally well for higher taxonomic groups. For example, a more practical approach depending on

727 the diversity of species and the taxonomic skills of the researchers would be to group species

728 according to a higher taxonomic level (e.g. Genus, Family) and to also consider growth form

729 (e.g. massive, branching, encrusting, corymbose) and reproductive mode (spawner, brooder).

730 The advantage with this approach is that uncertainty around the identity of species is obvious,

731 rather than records of incorrectly identified species becoming entrenched in the literature. Such

732 approaches are valid where the objective of management is to protect reef integrity by ensuring

733 resilience of the coral assemblage at a functional level.

734

735 **Inferring spawning and timing of sampling:** Sampling of the dominant corals must take place

736 throughout the potential reproductive seasons in order to determine the relative magnitude of

737 reproductive output throughout the year. A key factor in the logical process of determining

738 whether or not spawning has taken place is the construction of a series of data points through

739 time that demonstrates the development of gametes and their subsequent disappearance after

740 spawning. Oogeneic cycles in spawning corals take several months, so in species know to spawn

741 biannually (March, October) or over a protracted period (September to April) eggs will be

742 present in the population during most months. There is no evidence of corals spawning during

743 winter months, so detailed sampling in this period is not necessary. A sampling program to

744 determine the proportion of species and colonies spawning or releasing planulae throughout the

745 year should, however, span at least nine months from the start of spring to the end of autumn.

746 Preliminary sampling should be conducted monthly, and take into consideration the influence of

747 the lunar cycles. Ideally, sampling on Western Australian reefs should occur approximately one

748 week before the predicted night of spawning, providing the greatest amount of information on

749 the timing of spawning based on characteristics of gamete development; more than a week and

750 eggs may not yet be pigmented, while less than a week the chances of missing an early spawning

751 increases. The optimal time of sampling will depend on the assemblage. The presence of mature

752 (pigmented) eggs or larvae (in brooding species), and fully developed sperm, followed by their

753 subsequent disappearance, is the best basis for making strong inferences about the timing of

754 spawning. It is important to note that in many corals, particularly the Acroporidae, eggs may not

755 be pigmented more than two weeks prior to spawning and that unpigmented eggs may also be

756 spawned, highlighting the need for large sample sizes and for sampling to be conducted

757 following spawning events. In other taxa, particularly some Faviidae, eggs may be pigmented for

758 two months or more before spawning.

759 A single annual sample is a weak basis for inference, particularly when spawning is split or

760 staggered, for species that have protracted spawning seasons, or for brooding corals. It is vital

761 that accurate records of the exact timing of sampling are reported as metadata, in order for clear

762 conclusions to be drawn regarding the timing of spawning based on sequential sampling.

763  In addition to re-sampling the assemblage through time, tagged colonies would ideally be

764  resampled to strengthen inferences about the time(s) of spawning. This eliminates doubt about

765  whether the presence or absence of gametes is due to a spawning event, or due to variation in the

766  timing of spawning among colonies within a population; it is particularly useful for species that

767  spawn biannually. Consideration must obviously be given to the number of samples that can be

768  taken from a single colony, so as not to cause significant stress and divert energy investment

769  away from reproduction. We suggest that samples from individual colonies are therefore taken

770  strategically, according to the wider pattern identified in the population from which random

771  samples are also taken. For example, sampling an individual colony to determine whether it

772  participates in both a spring and autumn spawning, or in both months of a split spawning, rather

773  than during many months of the year.

774

775  **Sample size:** Sample sizes must be adequate for the purposes of the study and to account for the

776  background variation in reproduction among species within the community, among conspecific

777  colonies during a year, and among years. If all colonies are reproducing and spawn during the

778  same month, then the level of replication required is small – but considerable sampling is first

779  required to establish this trend and it is uncommon for many species on most reefs. Relying on a

780  fixed sample size for all species can become problematic when colonies spawn during different

781  months, different seasons, if stressed colonies are not reproducing, if they have separate sexes, or

782  if spawning during a year is split. Simulations carried out to assess the power of sampling to

783  detect reproductively mature colonies in coral communities (Styan & Rosser 2012) can provide

784  useful guidelines for designing sampling programs, after the underlying assumptions have been

785  reviewed and the background variance established in the context of the assumptions of the

786  simulation. The required replication can range from a few colonies per species when all spawn

787  synchronously over a few nights each year, to many more colonies for assemblages with mixed

788  patterns of reproduction during some years. For example, on a reef when 30% of the assemblage

789  is spawning in spring, many colonies per species will need to be sampled following the full

790  moon in October during a year of split-spawning (after the October spawning) so as not to

791  underestimate the significance of the event, especially if a proportion of colonies are not

792  reproducing due to environmental stress. Otherwise, insufficient sampling would not identify the

793 period as important and it may not be investigated in subsequent years when spawning was not

794 split and colonies not stressed.

795 It is important to note that the absence of eggs in a colony provides few insights into broader

796 patterns of reproduction, further highlighting the need for sufficient replication. At least 10 or

797 more colonies per species are therefore needed for adequate quantification of reproductive

798 patterns on WA reefs that do not mass spawn during a single month each year – however, the

799 replication required on each reef can only be determined after background variation in space and

800 time are first established. We argue that for most WA reefs it is better to first sample the most

801 abundant species rigorously to determine their pattern of reproduction, rather than sample most

802 species within low replication. Additionally, within colonies not all polyps may be reproductive,

803 so multiple samples from single colonies are advisable. For example, where both *in situ* and

804 microscopic examination of eggs are used to infer times of spawning in certain coral species (e.g.

805 staghorn *Acropora*), eggs may be observed in one method but not the other.

806

807 **Use of existing data and streamlining of sampling:** Studies based on the sampling design

808 principles above are rare, not only in WA but globally due to logistical demands. However, they

809 are necessary for environmental managers because there is insufficient knowledge of the

810 underlying reproductive biology of seasonality and within-population synchrony in coral species

811 at any given location. Where there is well documented information on seasonality and

812 synchrony, sampling may be streamlined. For example, when the species' annual gametogenic

813 cycle has been described and it has been shown that the population spawned with virtually 100%

814 synchrony during one lunar period of the year, sampling could be conducted immediately before

815 and after the predicted spawning window. However, for most species of coral in WA such

816 information is lacking, making more extended sampling periods necessary.

817 Once the community has been defined and the experimental design confirmed, methods that can

818 be used to determine the time of spawning or planulae release include: spawning observations,

819 recruitment to artificial substrata, *in situ* examination of gametes, microscopic examination of

820 gametes (immediate and preserved), and histological examination of gametes. The most

821 appropriate method depends on the question to be addressed, the region in which the reefs are

822  found and species being investigated, but a rigorous assessment usually combines multiple

823  approaches.

824

825  **Direct observations:** Direct observations to establish the date and time of spawning include

826  those made of colonies *in situ* or in aquaria (e.g. Babcock et al. 1994). *In situ* observations are

827  the most reliable way to confirm spawning, but are rarely conducted because the logistic

828  difficulties limit replication. The most useful way to apply *in situ* spawning observations is

829  therefore to combine them with data from previous reef surveys and *in situ* observation of

830  gamete development (see below). Aquarium observations present similar logistical issues, and

831  inflict some level of stress on colonies that potentially alters their time of spawning. The

832  approach has been used more successfully in brooding corals kept in aquaria for several months,

833  with the dates of planula release around lunar phases determined each day with the use of planula

834  collectors (e.g. Richmond & Jokiel 1984, Jokiel et al. 1985).

835  Another observational method used to provide information on the timing of spawning in coral

836  communities is visual surveys for coral spawn slicks, usually the morning after a spawning

837  event. While this method is useful for establishing that some spawning has occurred, the

838  approach cannot provide information on the scale of the spawning and the origin of the slicks is

839  unknown; the absence of a slick obviously provides no evidence of spawning having not

840  occurred. While all of these methods provide information about the time of spawning in a sub-set

841  of species, they alone are not sufficient to establish the community-wide patterns of reproductive

842  seasonality required for the purposes of managing environmental impacts.

843

844  **Coral recruitment:** Coral recruitment surveys can be used to inform the general timing of peaks

845  in reproduction (months/seasons) (Wallace & Bull 1982) but they do not precisely describe

846  temporal variation in peaks in reproduction. This is in part because pre-settlement larval periods

847  vary among coral, particularly spawning and brooding corals, and artificial substrata must be

848  deployed and retrieved in a set period ($\approx$ few weeks) before and after each spawning; the period

849  before is required to pre-condition substrata with algal communities and the period after is

850  required for larval metamorphosis and calcification to occur. Deploying and retrieving substrata

851  each month is logistically difficult and provides indirect, and relatively imprecise, information

852    about coral reproduction. A more precise identification of spawning times is usually required by

853    environmental managers. The link between coral reproduction and recruitment can also be

854    decoupled by unknown rates of larval mortality, current speeds and directions (Caley et al. 1996;

855    Edmunds et al. 2010; Hughes et al. 2000) and recruitment provides retrospective rather than

856    predictive insights into the times of reproductive output.

857

858    ***In situ* examination of eggs:** *In situ* examination of eggs is the most common and perhaps useful

859    means of determining times of spawning, provided certain criteria are met. If knowledge of the

860    proportion of colonies participating in a spawning event is required it is vital to know whether

861    the species are hermaphroditic or gonochoric (separate sexes), as eggs will obviously be absent

862    from male colonies. Eggs of gonochoric species are often small and relatively colourless

863    (Harrrison et al. 1990). Even where gonochoric species produce large coloured eggs, testes will

864    remain colourless or white and difficult to distinguish from the white skeleton of a coral

865    fragment. The sex ratio of gonochoric species must be known if the presence of mature

866    (pigmented) eggs in colonies is to be used to infer the proportion spawning. Thus, *in-situ* visual

867    examination of gonochoric species is more difficult and likely to lead to incorrect conclusions. It

868    is also vital not to sample the sterile tips or the edges of a colony, which have grown subsequent

869    to the initiation of gametogenesis in the rest of the colony (Oliver 1984; Wallace 1985).

870    Furthermore, is it very important to examine multiple polyps within each sample, and multiple

871    samples from each colony, as some polyps may be sterile or have low fecundity. These points

872    apply to whatever method of oocyte examination is to be employed.

873    *In situ* examination of eggs is most useful for branching corals that have large ($\approx$ >0.5 mm)

874    pigmented oocytes prior to (< 2 weeks) spawning that can be easily identified in the field (e.g.

875    *Acropora* spp.). Colonies are generally examined *in situ* several days prior to the predicted dates

876    of spawning. Maturity is examined in the field by breaking off coral sections to expose oocytes

877    (Harrison et al. 1984), and several sections should be examined if eggs are not initially observed.

878    Oocyte pigmentation is often used as an indication of maturity and timing of imminent

879    spawning. Egg colour varies with developmental stage from small unpigmented eggs (indicating

880    spawning is still some months away), to large pigmented eggs. Importantly, the size of mature

881    eggs and the degree and colour of pigmentation varies among species; when mature *Acropora*

882    eggs are typically pink or red, whereas the Faviidae may be blue or green, the *Montipora* may be

883    brown due to the presence of zooxanthellae, while other species may have cream eggs when

884    mature (Babcock et al. 1986; Harrison et al. 1990; Heyward & Collins 1985; Shlesinger et al.

885    1998). In *Acropora,* pigmentation may not occur until two weeks or less before spawning, in

886    some Faviidae eggs may be pigmented as much as two months before spawning, and species

887    such as *Acropora* and massive *Porites* have been observed to spawn unpigmented eggs (Babcock

888    et al. 1986; Harrison et al. 1984; Harrison et al. 1990; Mangubhai & Harrison 2007; Stoddart et

889    al. 2012), all complicating the use of egg colour as an indicator of imminent spawning. While *in*

890    *situ* visual observations have led to many useful inferences about the timing of spawning in coral

891    communities, they can be ambiguous and are best used as part of a sampling program that also

892    uses microscopic examination of eggs, and ideally the sequential sampling of tagged colonies.

893    Spawning times should also be confirmed by the disappearance of eggs from colonies following

894    the predicted date of spawning.

895

896    **Microscopic examination of gametes:** *In situ* examination of polyps is well supported by

897    microscopic examination of the samples on the same day. Such examinations should be

898    conducted on broken sections of coral under a dissecting microscope or with a hand lens, and can

899    reveal gonads that were not visible underwater. This is particularly useful for species with small

900    polyps and gonads, or those with a low fecundity (e.g. branching *Acropora*). Inferences about the

901    times of spawning are also improved by investigating the developmental stages of testes. When

902    testes are prepared and examined with a compound microscope (40 × objective), sperm shape

903    and motility can be observed. Testes enlarge markedly and sperm develop tails during the last

904    month before spawning. Sperm heads remain spherical until the last one to two weeks before

905    spawning, when they will become cone or acorn shaped, and a high degree of sperm motility

906    occurs a few days before spawning (Harrison et al. 1984). Microscopic examinations are more

907    time consuming, but always more reliable and informative than field observations alone.

908    Microscopic examination of gamete development can also be conducted on well preserved

909    samples, but only after the sample has been decalcified with acid. Egg colour and shape are not

910    retained following preservation and it is not possible to discern aspects of sperm morphology or

911    behaviour. Where the dimensions of mature eggs or testes are known for species being sampled,

912   measurements of their size can be can be used to make inferences about the likely time of

913   spawning. Several studies have quantified the size of eggs within replicate colonies of a species

914   at the time of spawning, and there can be variation in egg sizes within colonies and among

915   conspecific corals (Gilmour et al. 2016; Heyward & Collins 1985; Mangubhai 2009; Mangubhai

916   & Harrison 2007; Stobart et al. 1992; Wallace 1985; Wallace 1999). Egg size prior to spawning

917   can also vary considerably from year to year, and is not a reliable metric alone for determining

918   the month of spawning. Therefore, egg size can be used to estimate level of maturity and as an

919   indicator of spawning with accuracy of perhaps two months, but probably not for a single month

920   or less. Consequently, investigation of the preserved gametes is particularly useful for tracking

921   their development over several months leading up to a spawning event, but to determine the

922   month(s) spawning also requires *in situ* and microscopic examination as part of the sequential

923   sampling program.

924

925   **Histological examination of gametes:** Histology is used for corals that are not well suited to

926   field examinations, usually due to their morphology and their having small polyps and eggs that

927   are not easily visible with the naked eye (i.e. massive *Porites, Pavona*). Often these are also

928   gonochoric species with separate male and female colonies, for which histology provides the

929   only approach to describing the development of testes prior to spawning. This method is also

930   commonly employed to assess reproductive status of brooding corals and the presence of planula

931   larvae. Preparation for histological examination is time consuming and costly, and usually

932   involves decalcifying tissue, dehydration and fixing of samples in wax, and then sectioning and

933   mounting tissue to slides. Egg and testis development or presence of planula larvae can then be

934   assessed using previous work as guides (Szmant-Froelich et al. 1985; Vargas-Ãngel et al. 2006).

935   The development and growth of gonads and gametes can be tracked by measuring changes in

936   size as well as morphological developmental features like sperm shape through time. As with *in*

937   *situ* examination of gonads, sperm development stage is a particularly useful indicator of

938   maturity and imminent spawning. Gamete development stages are frequently used in describing

939   the reproductive status of corals sampled using histological methods, and also occasionally for

940   microscopic examinations of freshly sampled tissues. Gamete development staging should be

941   done with reference to published and accepted staging criteria available in the peer reviewed

942 literature, and clearly defined so that the unambiguous interpretation of staging by others will be

943 possible.

944

945 **Complementary methods:** The most informative studies of coral reproduction involve

946 sequential sampling of colonies using a combination of complementary methods. For example,

947 determining the times of spawning may involve monthly examination of eggs in preserved

948 samples. As eggs approach a size in which spawning is likely, then preserved samples may be

949 supplemented or replaced by *in situ* and microscopic examination of egg size and pigmentation,

950 as well as the size of testes and the stages of sperm development. When the night of spawning is

951 predicted within a given month, the *in situ* and microscopic examinations of eggs and sperm are

952 continued on a daily basis around the predicted nights of spawning, possibly supplemented by *in*

953 *situ* observations of spawning and evidence of spawn slicks the following day. On all reefs, a

954 proportion of species and colonies typically spawn over several nights, so continued sampling is

955 required to quantify the proportion of colonies without eggs and to identify the main night of

956 mass spawning within a period.

957 Great care should be taken to correctly record metadata and to correctly identify the main night

958 of spawning relative to the full moon, particularly to note instances when split-spawning has

959 occurred. Split-spawning typically occurs every few years and can occur over consecutive years,

960 and not recognising the phenomenon has biased the existing data for Western Australian reefs.

961 Also, supplementing these methods with tagged colonies that are sampled periodically through

962 time will give a better indication of whether split-spawning has occurred, whether assemblages

963 spawn biannually or over a protracted period, or whether species have overlapping gametogenic

964 cycles (e.g. *Turbinaria*). For gonochoric species with small polyps and gametes, or brooding

965 corals, this sampling approach will likely involve the use of histological analyses as well as *in*

966 *situ* and microscopic methods. These approaches are examples of applying multiple

967 complimentary methods, but the best approach will depend on the aims of the study, the region,

968 habitat, and species being investigated.

969

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

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

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

996 A lack of accurate and unbiased information about times of reproductive output by coral
997 communities impedes management initiatives aimed at reducing pressures to their early life
998 history stages. Managers would ideally be provided with quantitative estimates of the
999 reproductive output during different weeks, and even nights of the year, and its contribution to
1000 the long-term maintenance of populations. Obtaining this knowledge is logistically impossible

1001    until methods are developed that can easily quantify larval production, survival, connectivity,

1002    and per capita rates of recruitment per adult, for the most abundant species within a community.

1003    However, with far less effort it is possible to obtain relative estimates of reproductive output for

1004    coral communities in different months of the year. Mass spawning was originally defined as

1005    '…the synchronous release of gametes by many species of corals, in one evening between dusk

1006    and midnight...' (Willis et al. 1985),  taking place within a mass spawning period of up to a week

1007    following full moon on the Great Barrier Reef. There has since been debate about what

1008    constitutes a 'mass spawning' or a 'multi-specific spawning' on a reef, and a quantitative

1009    estimate of spawning synchrony has been developed (Baird et al. 2009) to assess biogeographic

1010    variation in spawning synchrony among species. Here we consider one approach to quantifying

1011    the significance of periods of reproductive output for coral communities on a reef, which

1012    combines the relative abundance of coral groups with the proportion spawning or releasing

1013    larvae during different months.

1014    To apply information on reproductive synchrony to the management of ecological processes,

1015    such as reproduction and recruitment in coral communities, it is necessary to quantitatively

1016    weight this information according to community composition. Community composition on a reef

1017    varies considerably among habitats (lagoon, reef flat, reef crest, reef slope) and among sites

1018    within these habitats, particularly on inshore reefs. The abundance of corals with different cycles

1019    and modes of reproduction also vary among these habitats and sites, so careful consideration

1020    must be made of the assemblage of corals that best characterises the reef when assessing its times

1021    of reproductive output (or the assemblage for which reproductive information is required). Here

1022    we define the community based on percentage cover data, which is regularly collected during

1023    monitoring programs across habitats and replicate sites. These data provide a less biased sample

1024    of the community composition than is often obtained during reproductive surveys and can

1025    provide unexpected insights into which coral groups are most common and whether their

1026    patterns of reproduction are well known. For example, knowledge of coral reproduction is often

1027    for the most conspicuous and easily sampled species of *Acropora*, whereas little reproductive

1028    data may exist for other species of spawning (e.g. *Montipora, Porites*) and brooding corals (e.g.

1029    *Isopora, Seriatopora*) that may have a similar relative abundance on a reef.

1030    Once the community composition has been quantified, a decision must be made about whether
1031    all taxa are to be included, or whether sampling effort can be reduced by excluding the rare
1032    corals. Although there are typically over tens of genera and hundreds of coral species on tropical
1033    coral reefs, many species are rare. For example, on Kimberley oceanic reefs there are over 35
1034    genera and 300 species of hard corals, but 10 genera contribute approximately 85% of the coral
1035    cover and five genera contribute approximately 65% of the cover. On reefs with less diversity,
1036    comparatively few species may contribute much of the coral cover. A 'community' may
1037    therefore be defined by the corals that make up most (e.g. >80%) of the total coral cover. An
1038    alternative to using a threshold of relative abundance is applying multivariate analyses to
1039    quantify the coral groups that best characterise, or distinguish, community structure through
1040    space and time, depending on the objectives of the study. Focusing on the detailed patterns of
1041    reproduction in the dominant species on a reef significantly reduces the sampling effort required
1042    to quantify temporal variation in reproductive output, as finding and sampling rare species with
1043    sufficient replication is most time consuming. Care must obviously be taken in deciding the
1044    threshold for including dominant species in a 'community' and the means by which they are
1045    categorised (e.g. family, genus, species, growth form), which will need to be reviewed as
1046    communities change and as more reproductive data are obtained.

1047    Further confounding assessments of the significance of reproductive periods on a reef is the
1048    identification of coral species. The issue is improved by considering only the most common
1049    species, but even these can be very difficult to distinguish. Variation in physical conditions
1050    among reefs and habitats, hybridization, reproductive isolation, and cryptic speciation make it
1051    impossible to correctly identify all of the colonies sampled during extensive reproductive
1052    surveys, and very few people are capable of correctly identifying most colonies correctly *in situ.*
1053    For example, many species of *Porites*, Faviidae, *Montipora* and *Acropora* are common on most
1054    tropical coral reefs, but within each of these taxa are many species easily confused *in situ*, even
1055    by experts. Errors in the identification of species will affect estimates of the number of species
1056    and the proportion of their colonies participating in a spawning, yet this can be the criteria by
1057    which the significance of spawning events is assessed. Inconsistent identification of species
1058    likely accounts for some apparent discrepancies in the times of spawning by species within
1059    regions of Western Australia presented here.

1060 It is also impossible to correctly identify all species when quantifying the composition of coral

1061 communities in monitoring programs, particularly from photographic or video stills. Broader

1062 taxonomic, morphological and life history groups are usually used in this context. Thus, when

1063 quantifying the significance of spawning events for coral communities, errors can be avoided and

1064 efficiency increased by grouping some species to a higher taxonomic level (Genera/Family), but

1065 also distinguishing these according to growth form (e.g. branching, corymbose, encrusting;

1066 Wallace 1990, Veron 2000) and reproductive mode (spawner, brooder; Harrison and Wallace

1067 1990, Baird et al. 2009). The approach is obviously not needed for species that are abundant

1068 and/or functionally important on a reef and easily identified (e.g. *Isopora brueggemanni*,

1069 *Seriatopora hystrix, Diploastrea heliopora*).

1070 Once the community of interest is defined and the relative cover of coral groups determined, the

1071 patterns of reproduction must be accurately quantified (see Section 3). The approach suggested

1072 here is to combine the community abundance and reproductive data to quantify relative estimates

1073 of reproductive output by the community throughout the year; it is therefore necessary to have

1074 both types of data for the same groups of corals. For example, in a hypothetical coral assemblage

1075 of two species, species A makes up 20% (relative) of the total coral cover and spawns only

1076 during October, and species B makes up 80% of the coral cover and spawns during March.

1077 Reproductive output for the community is therefore 20% during October and 80% in March. In

1078 this example, both species reproduce exclusively during a single month, whereas communities

1079 characteristically have species that spawn during two or more months a year, due to phenomena

1080 such as split-spawning, asynchronous spawning and within-population biannual spawning.

1081 Additionally, brooding corals release larvae over several months within a year. Here we use

1082 available data to apply the approach at two *hypothetical* reefs with contrasting coral assemblages

1083 and patterns of reproduction (Figure.2), which are similar to those at some oceanic and inshore

1084 reefs of Western Australia. The method for calculating reproductive output during each month is

1085 simple (Supplementary Table 4), but considerable sampling effort is required to produce accurate

1086 estimates of community composition and the proportion of colonies within each taxa reproducing

1087 each month (Section 3, Supplementary Table 4). Quantifying the proportion reproducing each

1088 month will usually require monthly sampling, or at least bimonthly, although less effort may be

1089 required after several years under a range of conditions and depending on the methods used.

1090    In a hypothetical example for an oceanic and inshore reef at north-western Australia, the monthly

1091    reproductive output differed according to their community composition and the cycles of

1092    reproduction within and among coral taxa (Figure 3). The main month of reproductive output at

1093    both reefs was March, but with more synchronous spawning in March at the oceanic reef and

1094    more protracted spawning over March and April at the inshore reef. At both reefs, over 40% of

1095    the communities reproductive output occurred during other months, but for different reasons.

1096    The oceanic reef had a higher (≈20%) reproductive output during spring (October/November)

1097    and particularly October than at the inshore reef (≈8%), due to a higher number of species

1098    spawning biannually, a higher abundance of *Acropora*, and a tendency for spawning to be more

1099    synchronous during a single month. There was a much higher reproductive output in December

1100    (22%) on the inshore reef, due to the abundance many massive *Porites* that spawn predominantly

1101    in December. During several other months of the year reproductive output was higher on the

1102    oceanic reef, due mainly to the many massive *Porites* spawning and brooding *Isopora* releasing

1103    larvae from spring to autumn. In contrast, the brooding corals in this example were rare on the

1104    inshore reef and the spawning over several months was restricted to the *Turbinaria*. These

1105    estimates of reproductive output for the oceanic reef and the inshore reef are hypothetical,

1106    intended only to provide a worked example.

1107

a)

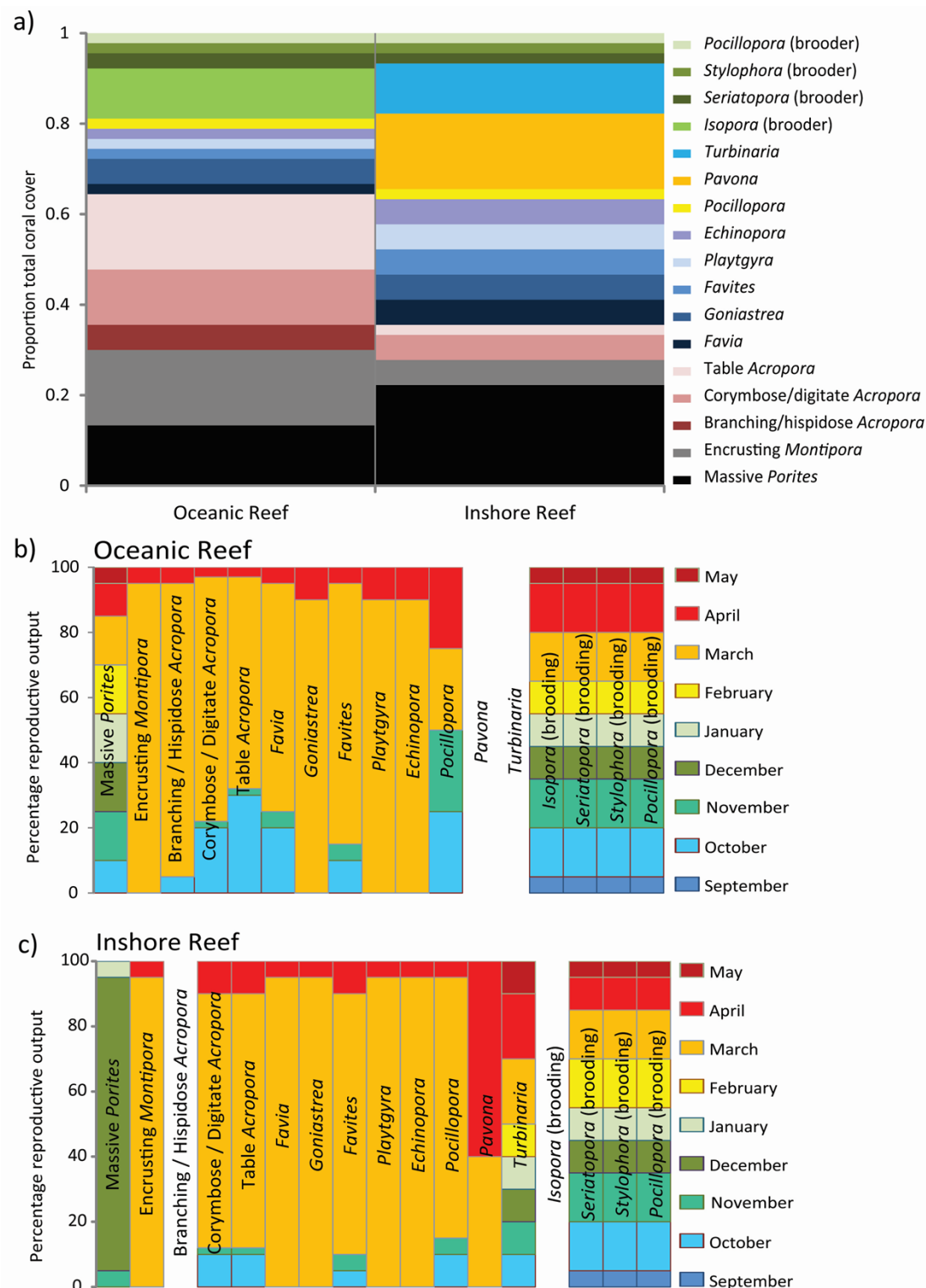
b) Oceanic Reef

c) Inshore Reef

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, *Povona* and *Turbinaria* were absent from the oceanic reef and *Isopora* absent from the inshore reef.

1108

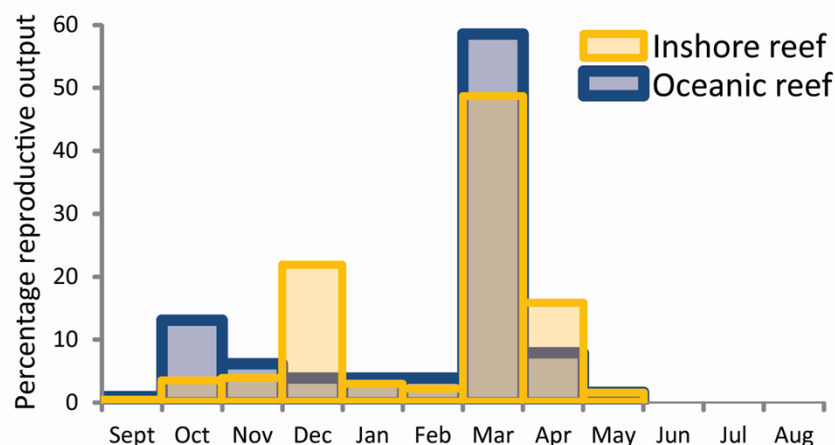



Figure 3. Percentage reproductive output during each month on a hypothetical oceanic and inshore reef at north-western Australia. Calculations are based on the relative abundance of coral groups within the community and the proportion reproductive output for spawning and brooding corals during each month of the year (Fig. 3; Supplementary Table 4).

1109

1110 This is one of several possible approaches to quantifying temporal variation in reproductive
1111 output for an entire community throughout the year, intended to aid management decisions. The
1112 approach is aimed at identifying the months in which significant reproductive output occurs at
1113 the scale of the entire community, and more detailed temporal sampling within these months is
1114 required to determine the nights of spawning and planula release relative to the phases of the
1115 moon. In the context of managing environmental impacts, the approach presented here has
1116 several limitations. Most significantly, by considering the reproductive output of the community
1117 as a whole, it does not sufficiently recognise the significance of periods of reproductive output
1118 by functionally important species with unique cycles of reproduction. For example, massive
1119 *Porites* on inshore reefs that spawn predominantly just a few nights after the full moon in
1120 December (Stoddart et al. 2012), or species on the oceanic reefs that may spawn exclusively
1121 during spring (Supplementary Table 4). Additionally, brooding corals may have a negligible (e.g.

1122    < 20%; Supplementary Table 4) proportion of planula release during the month and particularly

1123    main night of mass spawning on a reef, occurring around the full moon over several other

1124    months through the year.

1125    Importantly, the proportion of reproductive output each month will vary among years according

1126    to changes in community structure and particularly the occurrence of split-spawning or

1127    environmental stress. Consequently, several years of data collection are required to obtain a

1128    reasonable understanding of reproduction on the reef before sampling effort can be reduced. For

1129    example, it may be concluded incorrectly that reproductive output was not significant during

1130    March, the usual month of mass-spawning by coral on most Western Australian reefs, if

1131    spawning was split (March/April) or because environmental stress (e.g. poor water quality,

1132    cyclone damage or mass-bleaching) precluded reproduction. Another limitation of this approach

1133    is that the temporal resolution is presented to the calendar month, with the assumption that

1134    spawning occurs approximately one week after the full moon, whereas reproductive output in

1135    some spawning corals (e.g. Faviidae at Ningaloo Reef) and many brooding corals are likely to

1136    occur around the new moon. Furthermore, affording protection to only the main month of mass

1137    spawning and not in other months may have unforeseen consequences, such as affecting

1138    connectivity between reefs following spawning events in which oceanographic currents differ

1139    (Gilmour et al. 2009), or by reducing the genetic diversity of new recruits. This highlights the

1140    need to consider reproductive output for the entire community in the context of more detailed

1141    reproductive data for abundant or functionally important species of corals. Assessing the

1142    strengths and weaknesses of the approach requires a dedicated sampling design, on reefs with

1143    different coral communities through several years of environmental conditions. Other, and

1144    possibly better, approaches exists, however we present one here to formally introduce and

1145    hopefully build the concept.

1146

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