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# Extended periods of coral recruitment on the Great Barrier Reef

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**Abstract.** Highly synchronous spawning of many coral species followed by rapid settlement of larvae should result in a brief annual influx of recruits onto reefs. Here, we show that contrary to this prediction, *Acropora* recruits were recorded in every two-month interval over a two-year study period on settlement tiles placed on patch reefs in the lagoon of Walker Reef on the Great Barrier Reef (GBR). Nonetheless, recruitment in some taxa was seasonal. In the first year, recruitment of the broadcast spawning genera *Acropora* peaked in December, coinciding with the annual mass spawning period on the GBR. In the second year, there was a six-month period of high recruitment beginning in October. This extended recruitment most likely resulted from either long-lived larvae or larvae produced by *Acropora* colonies that spawn later in the season. In contrast, recruitment of the brooding genera, *Pocillopora*, *Stylophora* and *Seriatopora* occurred throughout the year reflecting the fact that these taxa planulate throughout the year in the central GBR.

**Key words:** coral reef, dispersal, spawning synchrony, recruitment, reproduction

## Introduction

Large fluctuations in recruitment are characteristic of marine organisms with a planktonic larval stage. High fecundity combined with heavy mortality in the plankton means that relatively small changes in the rate of mortality or the length of the planktonic phase can have major effects of the numbers of offspring available (Underwood and Fairweather 1989). Recruitment fluctuations of marine organisms are important for regulating populations and mediating species coexistence (Caley et al. 1996). In addition to understanding population dynamics, knowledge of recruitment patterns is a prerequisite for the effective management of marine ecosystems, enabling informed responses to disturbances, such as crown-of-thorns starfish outbreaks, storms and bleaching events (Pearson 1981; Almany et al. 2009).

In many species, recruitment is highly seasonal. Seasonality in recruitment has many important implications, for example the rate of reef recovery following disturbance will be influenced by the season in which the disturbance occurs (Rogers 1993). This seasonality is very striking in corals on the Great Barrier Reef (GBR), where a brief annual reproductive season in many species of corals combined with rapid settlement leads to prominent peak in influx of new recruits (Harrison and Wallace 1990). Typically, the densities of recruits are an order of magnitude greater on plates placed in summer than on those placed in winter (Hughes et al. 2002). The summer peak is most pronounced in the Family Acroporidae. Acroporid recruits typically comprise 80-90% of summer counts in the central and northern sections of the GBR, yet are virtually absent from winter samples (Wallace 1985, Fisk and Harriott 1990). Small numbers of acroporid recruits on winter plates (e.g. Harriott 1985) are presumed to be the genus *Isopora* which release planulae throughout the year at some locations (Kojis 1986). A similar seasonal trend is apparent in other broadcast spawning taxa such as the Poritidae (Harrison and Wallace 1990). In contrast, many pocilloporids release planulae throughout the year, depending on location, (see review in Tanner 1996) and pocilloporid recruits dominate winter settlement plates on the GBR (Wallace 1985) whereas they only comprise 10-20% of recruits on summer plates (Wallace 1985, Fisk and Harriott 1990). Elsewhere in the Pacific, pocilloporids dominate samples throughout the year (Hughes et al. 2002).

However, at a finer temporal scale than the 4-6 month plate exposure typical of most studies (Hughes et al. 2002) there is some variation in the summer peak in recruitment on the GBR. Babcock (1988) exposed consecutive sets of plates for two-week intervals in the months following the mass spawning period (Willis et al. 1985) at Bowden Reef in 1987-88. Surprisingly, there was no peak in settlement of acroporids following the mass spawning and settlement of acroporids was highest between mid-January and March (Babcock 1988). When this sampling design was repeated at Davies Reef in 1991-92, a pronounced peak in the recruitment of acroporids occurred in the two December samples, with densities of acroporid spat an order of magnitude higher than those on the January plates (Babcock 1992). Thus, two patterns of recruitment of spawning taxa emerge: heavy settlement dominated by acroporids immediately following the mass spawning period (Babcock 1992); or light settlement dominated by pocilloporids (Babcock 1988). Babcock (1988) hypothesized that the pattern on Bowden Reef in 1987 was atypical and was caused by strong winds prevailing at the time of the mass spawn.

More recent work on the length of the reproductive season in the *Acropora* on the GBR has revealed that there are many species that spawn much later in the summer than was previously appreciated (Baird and Guest 2009; Baird et al. 2009a & b). In addition, detailed research on the patterns of skeletogenesis in juvenile corals indicates that the maximum taxonomic resolution of coral recruits is achieved in the first two months of life (Babcock et al. 2003). Similarly, recent work on the length of the larval phase in broadcast spawning corals on the GBR has revealed that a small proportion of the larval cohorts of many species can survive for many months (Graham et al. 2008) and still complete metamorphosis (Connolly and Baird 2010). Consequently, the design of many earlier studies was not optimized to maximize taxonomic resolution of the recruits or to test for finer temporal patterns in the abundance of recruits, including the possibility of an extended period of recruitment for broadcast spawning species. Consequently, the aim of this study was to revisit seasonality in coral recruitment on the GBR using a shorter period of deployment of settlement substrata to increase the temporal and taxonomic resolution of these patterns.

## Material and Methods

The study location was Walker Reef (18° 19'S, 146°45'E), 52 km off the north east coast of Australia on the GBR. Six bommies of similar size, benthic structure, and degree of isolation were selected for the recruitment study. Bombies were 200-500m apart in 3m of water at low tide. The sampling unit consisted of a "stack" of five 20 x 20cm ceramic tiles threaded onto a central rod attached to a besser brick, glazed side up, positioned horizontally with 5cm PVC spacers in between each plate. Four stacks were positioned at the four corners of a diamond on each bommie. Between March 1993 and June 1995, sets of plates were sequentially deployed on the reef for 60-day periods, resulting in 12 "soaks". The total number of tiles was 120 at each soak (5 plates x 4 stacks x 6 bommies) and therefore 12 x 120 = 1440 settlement plates were deployed in total. On retrieval, the tiles were bleached to remove soft tissues and filamentous algae, rinsed in fresh water and dried. The upper and lower surfaces of each tile pair (800 $cm^2$ per tile) were censused for juvenile corals using a stereo dissector microscope at 10X magnification and identified to the following taxonomic level following Baird and Babcock (2000) and Babcock et al (2003): *Acropora*, *Isopora*, *Pocillopora*, *Seriatopora*, *Stylophora*, brooding *Porites*, spawning *Porites*, fungiids and "others".

## Results

Total coral recruitment was generally higher in the summer months between October and March, with the exception of a peak in recruitment of 16.6 ± 0.64 recruits per panel in the May-June soak in 1994 (Fig. 1). This peak was caused by an exceptionally high abundance of *Pocillopora* recruits (Fig. 1) and to a lesser extent *Stylophora* recruits (Fig. 1). Recruitment of *Acropora* was overwhelmingly concentrated in the warmer months, from October to March, with very few recruits between April and September (Table 1; Fig. 1). The overall abundance of recruits was similar in the two six month warmer seasons; 1102 spat settled in the October to March period in 1993-94 and 1129 spat settled in the October to March period in 1994-95 (Table 1). In the first warm season there was a significant peak in the October-November soak with a mean of 8.7 ± 1.06 recruits per panel (Fig 1b). *Acropora* recruitment was much more even in the second warm season (Fig. 1). Nonetheless, some *Acropora* recruits were found in every soak (Table 1). *Pocillopora* recruitment was much less seasonal than for *Acropora*. The prominent feature was a large pulse of recruits in May-June 1994 and lesser peaks in August-September 2003 and October-November 1994 (Fig. 1). *Stylophora* had a similar pulse of recruitment in May-June 1994 and recruits were consistently more abundant between October and January in both years (Fig. 1). *Seriatopora* recruitment was generally higher in the October to March soaks in both years with a peak of 1.6 ± 0.2 recruits per panel in December 1994 (Fig. 1). *Isopora*, brooding *Porites*, spawning *Porites*, "other' recruits and fungiids were too low in abundance for meaningful analysis of seasonal patterns (Table 1).

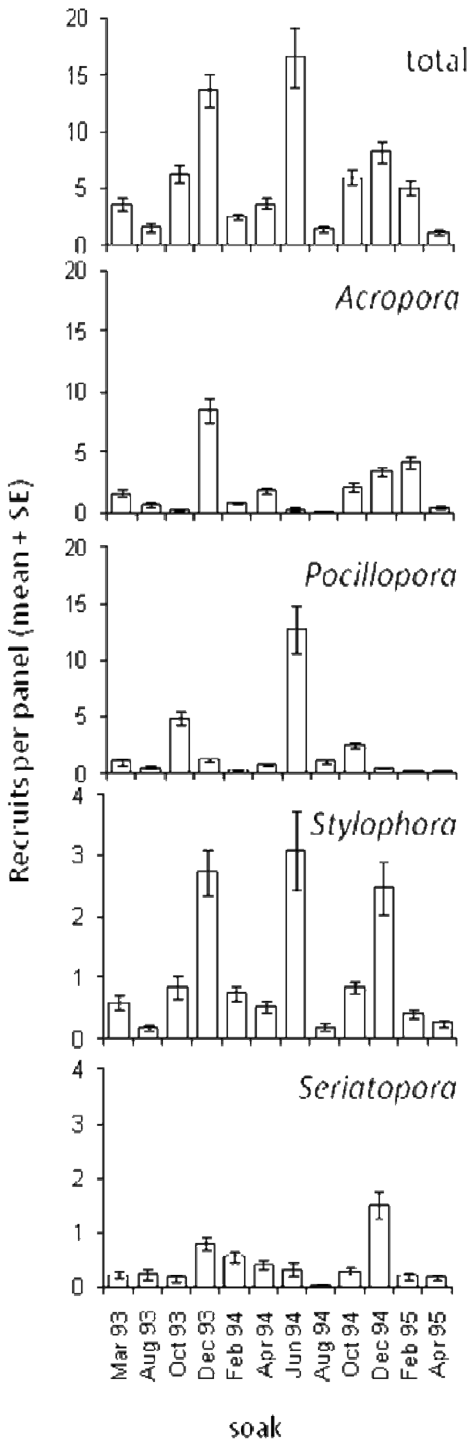


Figure 1: The mean abundance (± SE) of coral recruits in each of 12 soaks.

## Discussion

Seasonal patterns in recruitment generally match those predicted on the basis of known breeding patterns and life histories. Recruitment of the broadcast spawning genera *Acropora* was highly seasonal with peak abundance in the months coinciding with the peak reproductive season of these genera from October to November on the GBR (Baird et al 2009b). In contrast, recruitment of the brooding genera *Pocillopora*, *Stylophora* and *Seriatopora* was less seasonal, corresponding to the longer period over which planulae are released in the central GBR (Muir 1984; Schmidt-Roach and Warner pers. comm.). In addition to the difference in the length of the reproductive season, the larvae of species that brood are typically ready to settle on release, whereas broadcast spawning species have an obligate planktonic period of between three days and two weeks (Connolly and Baird 2010). Consequently, pulses in recruitment in brooding species are much more likely to be affected by environmental conditions prevailing at the time of release, such as extended periods of slack water, or hydrodynamic feature that aggregate larvae. This may explain the unpredictable peaks in recruit abundance seen in *Pocillopora* and *Stylophora* (Fig. 1). Nonetheless, recruitment of *Seriatopora* and *Stylophora* was high in December and *Pocillopora* high in October in both years and suggesting the reproductive output of these taxa may peak at these times (Fig 1).

The one unusual aspect in these patterns of recruitment was the extended period of high recruitment of the *Acropora* between October 1993 and March 1994. Until recently, it was generally accepted that the vast majority of *Acropora* reproductive activity was concentrated in a brief annual mass spawning period (Harrison and Wallace 1990; Willis et al. 1985). However, spawning in *Acropora* assemblages is not as synchronous as typically portrayed for the GBR (Baird et al. 2009b). On the GBR, a number of *Acropora* species spawn outside of the mass spawning period. For example, in a two year study of 9 *Acropora* species on Big Broadhurst Reef in the central GBR, *A. granulosa* spawned in March, four months after the mass spawning period, and some colonies of *A. sarmentosa* were mature in February, August and November (Wallace 1985). Furthermore, in a three-year study of spawning times in 12 morphospecies of the *Acropora humilis* group, a second substantial spawning event occurred three months after the November mass spawning period, with 11 of the 12 taxa participating in both events (Wolstenholme 2004). Colonies of *A. samoensis* spawned in December, January and February; the majority of colonies of *A. digitifera* spawned in February, and mature colonies of

| soak | Acrop. | Pocillop. | Styloph. | Seriatop. | Isop. | *Porites* brood | other | *Porites* spawn | fungiid | total |
|---|---|---|---|---|---|---|---|---|---|---|
| Mar-93 | 69 | 53 | 17 | 24 | 2 | 0 | 0 | 2 | 0 | 167 |
| Aug-93 | 18 | 471 | 80 | 17 | 6 | 7 | 2 | 11 | 0 | 612 |
| Oct-93 | 815 | 115 | 262 | 77 | 21 | 4 | 5 | 2 | 4 | 1305 |
| Dec-93 | 109 | 39 | 93 | 74 | 5 | 0 | 1 | 0 | 0 | 321 |
| Feb-94 | 178 | 77 | 50 | 40 | 4 | 2 | 0 | 3 | 0 | 354 |
| Apr-94 | 31 | 1223 | 297 | 32 | 0 | 4 | 2 | 0 | 0 | 1589 |
| Jun-94 | 13 | 104 | 18 | 4 | 0 | 0 | 0 | 1 | 1 | 141 |
| Aug-94 | 6 | 83 | 28 | 5 | 1 | 4 | 1 | 0 | 0 | 128 |
| Oct-94 | 400 | 403 | 134 | 53 | 14 | 7 | 10 | 1 | 1 | 1023 |
| Dec-94 | 327 | 43 | 237 | 146 | 21 | 1 | 4 | 2 | 2 | 783 |
| Feb-95 | 402 | 21 | 39 | 20 | 2 | 1 | 2 | 0 | 0 | 487 |
| Apr-95 | 43 | 21 | 25 | 18 | 0 | 0 | 0 | 0 | 0 | 107 |
| Total | 2411 | 2653 | 1280 | 510 | 76 | 30 | 27 | 22 | 8 | 7017 |

Table 1. The number of coral recruits in each of 12 soaks. Soak length was two months except for the first soak which was for approximately four months from March to July 1993.

*A. gemmifera* were present over a four month period (Wolstenholme 2004). Similarly Baird et al. (2009b) recorded some reproductive activity in *Acropora* assemblages every month from October to February in a cross shelf transect on the GBR. Clearly, an extended reproductive season in many *Acropora* species could result in an extended period of coral recruitment, at least in some years (Fig. 1).

An alternative explanation for an extended period of recruitment in the *Acropora* is the length of the larval phase. Many species of coral larvae are likely to be able to remain in the plankton for periods exceeding 100 days (see review in Graham et al. 2008) and a small proportion of these can complete metamorphosis (Connolly and Baird 2010). Consequently, recruits recorded in February-March could conceivable have originate from colonies that spawned in November or December. However, the effects of mortality and dilution of larvae after three to four months in the plankton suggest that this is likely to be much less influential on the abundance of recruits than an extended breeding period. Nonetheless, the observation that some *Acropora* recruits were recorded in all soaks indicates that an extended plankton duration is an important feature of coral larval recruitment.

Studies of coral settlement and recruitment are becoming more numerous for a variety of reasons. Firstly, reef scientists and managers have become more aware of the importance of monitoring processes such as recruitment rather than just changes in adult abundance in order to understand how reef ecosystems function. Secondly, early stages in the life history of corals are often more susceptible to certain environmental perturbations, such as eutrophication and sedimentation, than adults. Consequently, measuring changes in patterns of coral recruitment can provide an early warning of potential changes in reef resilience.

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