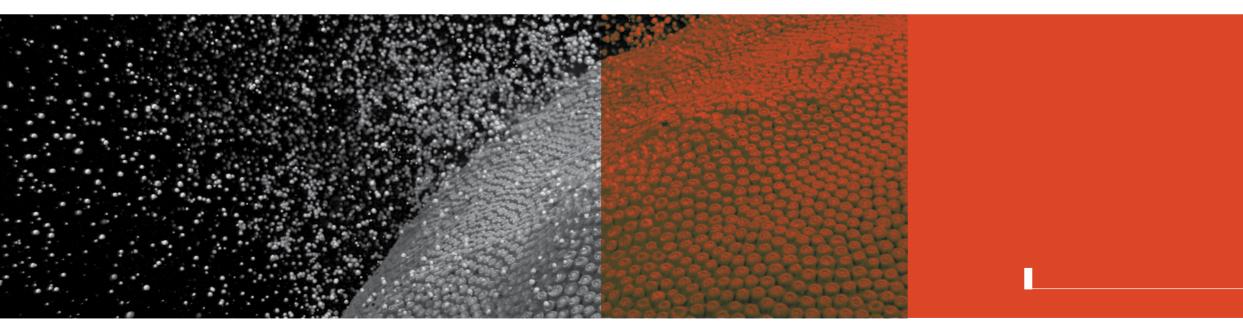
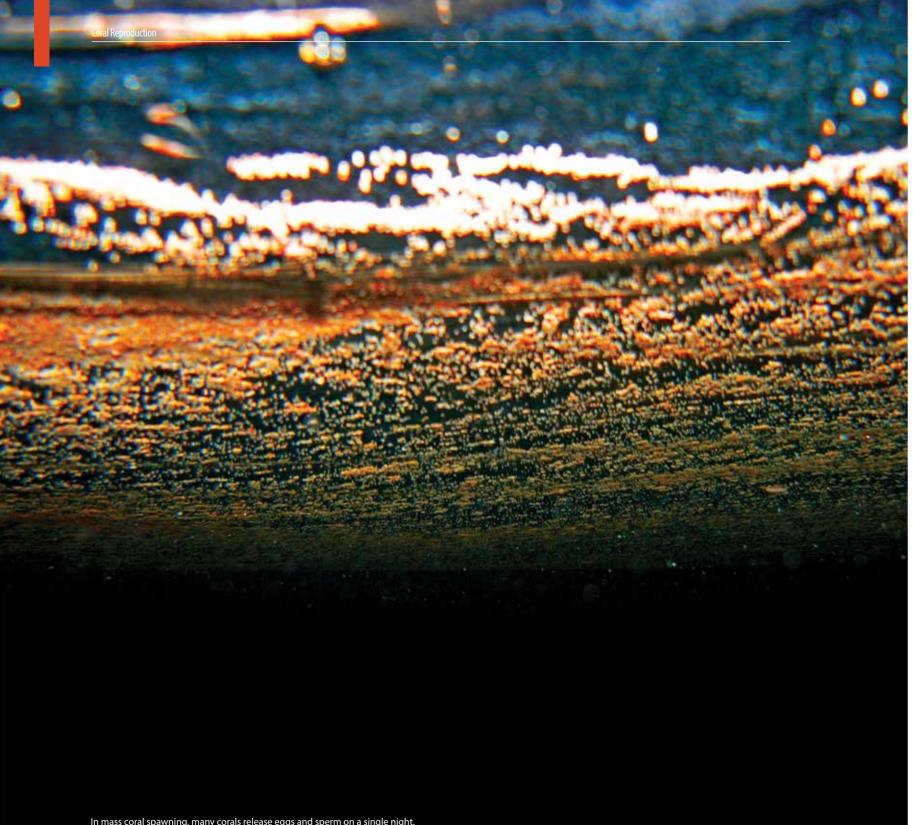
CORAL ECOLOGY



Coral Reproduction



On a single night following a full moon in spring and autumn, the sperm and eggs of many thousands of corals fill the ocean surface around Scott Reef. These mass spawning events are a remarkable sight — the billions of eggs have been described as rising through the sea like champagne bubbles. The next day they can be seen on the ocean's surface as massive slicks of coral spawn. This spectacular mode of reproduction represents a crucial and potentially vulnerable moment in the lifecycle of corals. Detailed studies conducted by scientists working at Scott Reef have provided important information about coral reproduction and spawning that can help guide the management and conservation of the reef ecosystem.

A spring surprise

Thirty years ago, on the Great Barrier Reef, scientists first recorded the mass spawning of corals. This finding overturned a long-held belief that most coral species reproduced by fertilising eggs within their polyps, where the resulting larvae were brooded until they were ready to settle. In fact, it is now clear that around 80 per cent of coral species reproduce by broadcast spawning, where larvae develop in the water following the release of both eggs and sperm.

Following this discovery, mass coral spawning was also documented on some of Western Australia's most iconic reefs, including Ningaloo Reef and the Abrolhos Islands. But unlike the Great Barrier Reef, mass spawning on these west-coast reefs takes place in autumn, rather than spring.

Later, in the 1990s, scientists working at Scott Reef and the Rowley Shoals confirmed that many coral species at these locations also spawned during autumn, in March or April, depending on the timing of the full moon. But further sampling in the 2000s turned up a surprise. In addition to the autumn mass spawning, a second, smaller spawning event was discovered in spring, usually in October, at a similar time to the events on the Great Barrier Reef. Since then, more than 75 species of corals have been sampled at Scott Reef, of which more than half have been documented to spawn in spring. However, very few of these species spawn only in spring, with most spawning during both seasons.

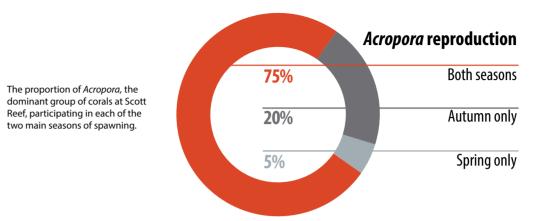
The most abundant species of corals at Scott Reef are in the genus *Acropora*, and it is their patterns of reproduction that are best understood. Of the *Acropora* studied so far, scientists have found that around 20 per cent of species reproduce only in autumn, another five per cent reproduce only in spring, while approximately 75 per cent do so in both seasons.

Spring spawning has since been documented on other Western Australian reefs north of Ningaloo, and the phenomenon of a primary and secondary spawning event has been documented at other reefs around the world.

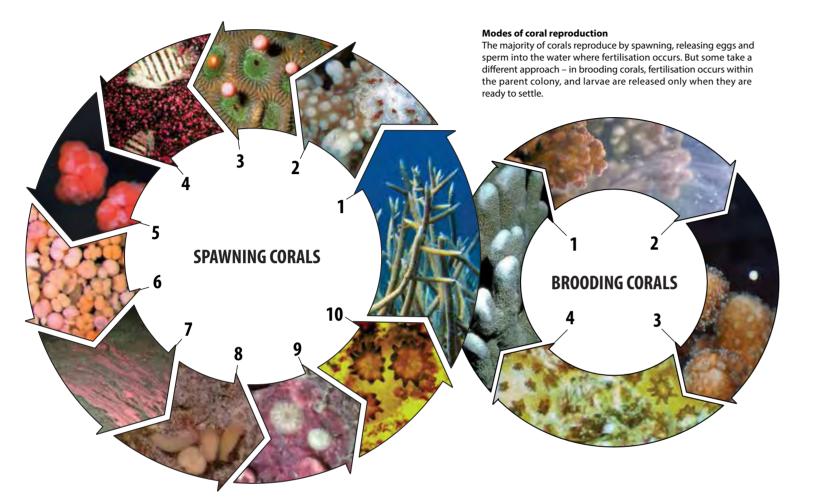
In mass coral spawning, many corals release eggs and sperm on a single night. The eggs float to the ocean's surface and aggregate as huge slicks of coral spawn.

The release of buoyant egg and sperm bundles from a colony's polyps at the time of mass spawn is one of nature's most spectacular events. Many colonies and species release eggs and sperm wi a few hours of each other, with a range of other organisms also participating in the event.

The Acropora are the most diverse and abundant corals at Scott Reef, and their many species have a wide range of shapes and colours. Most Acropora participate in the reef's mass spawning events in both autumn and spring, although a much larger proportion of colonies spawn in autumn.







Spawning corals

1. Maturity: Once a coral colony has reached a large enough size it becomes a reproductive adult.

- 2. Gamete development: Within the coral's many polyps, eggs develop over several months and sperm over several weeks.
- Spawning: When fully developed, the eggs and sperm are released from the colony, often synchronously in spectacular mass spawning events.
- 4. Predation: Various predators feed on the rich feast of eggs and sperm.
- 5. Fertilisation: Many corals release their eggs and sperm in compact bundles, which float to the water's surface before separating. Amid this soup of gametes, fertilisation relies on sperm locating the eggs from another colony of the same species.
- Cell division: Following fertilisation, eggs undergo a series of divisions through the different stages of embryogenesis before becoming larvae after approximately 24 hours.
- 7. Dispersal: Coral embryos and larvae form slicks on the water's surface. However, a day after spawning many of the viable larvae have already dispersed into the water column where they remain for at least two days before they are ready to settle. Some larvae may survive drifting in the water column for weeks before reaching a suitable reef habitat.
- 8. Settlement: Once ready to settle, and in the vicinity of a suitable patch of reef, larvae actively search the substrata for a site of attachment. The site they choose is critical, as they remain attached to this spot for life.
- Metamorphosis: Once attached, larvae commence metamorphosis, taking on the characteristic form of a coral polyp.
 Polyp budding: The coral polyp begins to excrete a calcium carbonate skeleton, and the colony grows through the repeated division of its polyps.

Brooding corals

- Maturity and gamete development: As with spawning corals, the brooding corals must grow to a size at which they become reproductive adults. Many brooding corals tend to be either male or female, producing either eggs or sperm within their polyps, in contrast to spawning corals that are often hermaphroditic, producing both eggs and sperm within their polyps.
- 2. Fertilisation and larval development: Mature brooding corals release sperm into the water column, which reach another colony and fertilise the eggs within its polyps. The fertilised eggs develop into embryos and then larvae, and the larvae are then 'brooded' within the polyp for several weeks. This process may occur several times a year in brooding corals, whereas most spawning corals produce eggs and sperm only once each year.
- Larval release: When developed, the brooded larvae are released by the polyps. Because most are ready to settle when released, the brooded larvae disperse over much shorter distances than the larvae of spawning corals that develop in the water column.
- Settlement to polyp budding: As with the spawning corals, the larvae of the brooding corals attach to the substrata, undergo metamorphosis into a coral polyp, and then grow through polyp division.

What triggers mass spawning?

From an evolutionary perspective, mass spawning is thought to increase fertilisation success and reduce the likelihood of eggs being eaten when released, through 'predator saturation' – predators can only eat a small proportion of the billions of eggs released in one night. Exactly what environmental conditions trigger the timing of the mass spawning events remains uncertain. Changes in water temperature and the number of daylight hours are thought to influence the months in which gametes develop and mature. Within these months, the nights of spawning at Scott Reef typically occur following a full moon and during neap tides.

A complex interaction between evolutionary and contemporary environmental conditions evidently determine the number of corals and species participating in mass spawning events within a year. Research at Scott Reef has added detail to this understanding. Importantly, scientists have found that although many species of *Acropora* spawn during two seasons each year, individual colonies appear to participate in only one of the two events – over several years of sampling individual colonies, there was no evidence of them spawning twice a year or switching from one season of spawning to another.

Remarkably, even neighbouring colonies of the same species, experiencing the same environmental conditions, have been found to consistently spawn at different times of the year, suggesting it may be genetic differences that determine the time of spawning for a particular coral colony. Recent analyses have identified significant genetic differentiation between groups of colonies of the same species that spawn during the different seasons, far greater than the genetic differences between colonies on reefs separated by several hundred kilometres. These results raise the question of how often colonies of the same species, which reproduce during different seasons, interbreed.

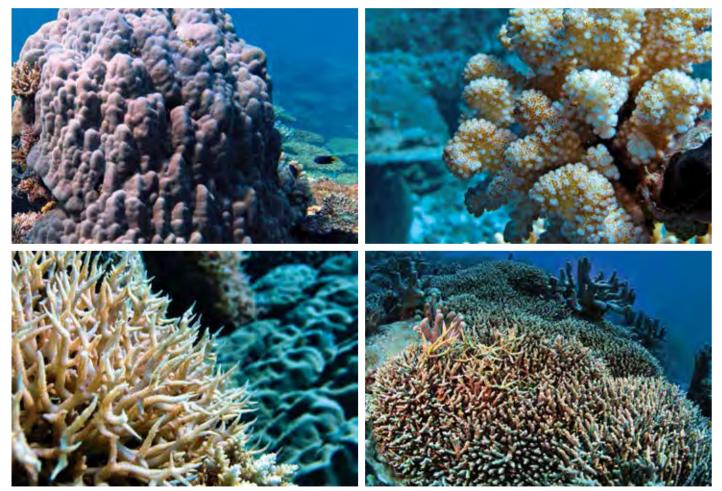


At Scott Reef, adjacent corals of the same species (blue and green colonies, above), experiencing the same environmental conditions, consistently spawn during different seasons. Recent work suggests that genetic, rather than environmental, factors determine the season of spawning for coral colonies at Scott Reef.

Exceptions to the rule

Although most of the corals at Scott Reef spawn during one of two months, some abundant and functionally important corals reproduce at other times of the year and their cycles of reproduction are not well described. The massive *Porites* colonies that contribute significantly to the structure of Scott Reef spawn more than once throughout the year, as do the many colonies of *Pocillopora verrucosa*, although it remains unknown if individual colonies spawn more than once a year.

In contrast to the spawning corals, the many brooding corals at Scott Reef tend to have multiple cycles of reproduction throughout the year. Reproduction in brooding corals involves the release of sperm that fertilise the eggs within the polyps of another colony. Larvae then develop while still in the polyps and are released several weeks later, when they are ready to settle. Some brooding corals are particularly abundant at Scott Reef, including the extensive thickets of *Isopora brueggemanni*, or the finely-branching *Seriatopora hystrix*, and produce larvae over several months around the two mass spawning events in spring and autumn.



Some common and functionally important corals reproduce in ways different to most others at Scott Reef. The massive *Porites* (top left) and *Pocillopora verrucosa* (top right) release their eggs and sperm in many months of the year, not only during mass spawning events. The brooding corals *Seriatopora hystrix* (bottom left) and *Isopora brueggemanni* (bottom right) release larvae over several months of the year.

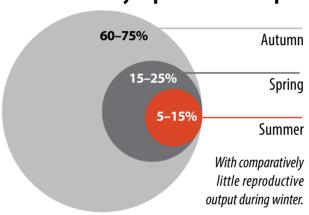
Conservation and management

Detailed information about the patterns of sexual reproduction in corals at Scott Reef is important for their management and conservation. Sexual reproduction underpins the maintenance of coral communities and their recovery from disturbances, yet these early stages of the life cycle are particularly susceptible to environmental stresses.

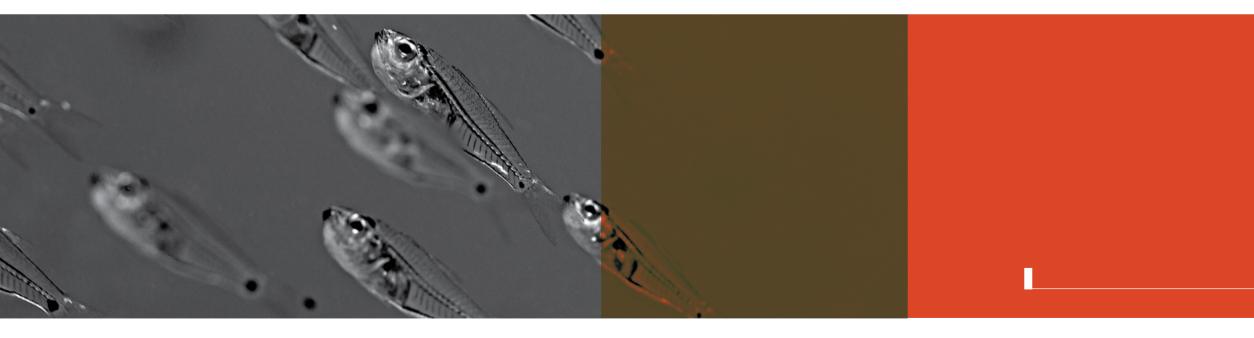
However, simply counting the number of species that participate in a spawning event provides little information about how important its contribution is to community maintenance. Estimating the significance of reproductive periods during the year requires information on both reproduction and the abundance of species, but for many reefs this combination of data is remarkably rare. At Scott Reef, researchers have combined estimates of abundance with information about reproduction in spawning and brooding corals to assess which periods contribute most to reproductive output.

As expected, more than 60 per cent of the reproductive output for spawning corals occurred during autumn, compared to less than 30 per cent in spring. However, a larger proportion of reproductive output for a few species of spawning corals, such as the massive *Porites* or those spawning only in spring, occurred during months outside of autumn. Similarly, the reproductive output for most brooding corals was much lower in autumn than in all the other months combined. Considering the entire community of spawning and brooding corals, between 60 and 75 per cent produced larvae during autumn, between 15 and 25 per cent in spring and between five and 15 per cent in summer, with little evidence of larval production in winter months. These proportions vary between communities and from one year to another, depending on the timing of spawning events and the relative abundance of different species. Further work will provide more insight into the degree of spawning synchrony among species and colonies within these seasons and the reasons for the observed variation among years.

Understanding the modes and timing of larval production for corals at Scott Reef is important, as they influence the distance and direction of larval dispersal. As winds and currents at Scott Reef vary between months and seasons, the timing of reproduction can determine whether larvae remain on the reef, or leave Scott Reef and begin the long journey north or south to another reef system. The pattern of reproduction is the first factor influencing larval connectivity among coral reefs of the region.



Community reproductive output



Larval Connectivity

Scott Reef and its neighbours are separated by wide expanses of open ocean. Whether the reefs are connected by larvae regularly traversing these expanses, or not, has important consequences for the reefs' ability to recover from disturbances.

Scott Reef may be hundreds of kilometres from mainland Australia, but it is not entirely alone in the expanse of the Indian Ocean. Just 25 kilometres to the north is Seringapatam Reef, a close neighbour, while a few hundred kilometres away are Ashmore Reef to the north and the Rowley Shoals to the south. Understanding exactly how the communities of corals, fishes and other living things on these reef systems are connected has been an important puzzle for researchers. Are successive generations of organisms at Scott Reef only produced by local adults, or are some the products of neighbouring reef systems that have travelled as larvae through the open ocean? This question is difficult to answer, yet has critical implications for how reefs recover from damage, and how they should be managed.

A matter of survival

When faced with damage from coral bleaching, cyclones or other severe disturbances, do Scott Reef and the other oceanic reefs off Western Australia stand together, or alone?

If reefs are 'open', meaning they are connected reproductively to other reefs, then a supply of larvae from one may aid recovery from damage at another. If, on the other hand, they are 'closed' systems with little larval exchange, then recovery from a severe disturbance will depend only on local survivors.

Considering that more than 80 per cent of coral species are known to reproduce by broadcast spawning – sending billions of larvae out into the ocean where currents can carry them to new locations – it was once assumed that most coral reefs were open systems, routinely connected to other reef systems over distances of tens to hundreds of kilometres.

More recent research has altered this view. Scientists now realise that although coral larvae can survive to disperse through the ocean for several weeks, they are ready to settle within a week of spawning, and are likely to do so provided they are near suitable reef habitat. Additionally, the vagaries of the open ocean and the risks of predation mean many of the larvae that disperse for long periods may never survive to settle elsewhere. Consequently, most coral larvae settle far short of the maximum distance they are capable of travelling.

Unlike continuous reef systems such as the Great Barrier Reef, Scott Reef and its neighbouring reef systems are extremely isolated. For larvae originating from these reefs, travelling beyond the reef means crossing many kilometres of open ocean before reaching another reef. Their chances of surviving such a journey are very low.

Larval Connectivity



Brooding fishes, such as the wolf cardinalfish (Cheilodipterus artus), protect their eggs from predation by carrying them in their mouths until they reach the larval stage.

Fish larvae are strong swimmers for their size, and are often found several kilometres from the reef in the open ocean where they grow, feed and develop until ready to settle.

Seringapatam Reef lies just 25 kilometres to the north of Scott Reef. The degree of larval exchange between these reefs is not known, but it is likely to be much higher for fish larvae than for corals, given their longer larval duration and superior swimming and sensory abilities.

> After spending weeks in the water column, the fully developed larvae return to the reef to settle and become juveniles. Some fish larvae have excellent sensory abilities, and use ocean currents to assist their return.

Most likely Movements of larvae Least likely

> Brooding corals, such as Seriatopora hystrix, have eggs that are fertilised while still inside the parent's polyps. The resulting larvae are ready to settle when they are released. Most settle less than a few kilometres from their parent colony.



Larval dispersal

Most corals and fishes undergo a larval stage, when they leave their parents and disperse through the water before settling at their new home. Understanding the distances and direction of larval dispersal is critical to managing coral reefs, but is extremely difficult to measure directly. Instead, scientists combine a variety of other information to determine the likely end points of the larvae's journey.



Spawning fishes, such as the bicolour chromis (*Chromis margaritifer*) release eggs and sperm into the water column. The eggs are fertilise d the larvae develop while in open water, receiving no parenta

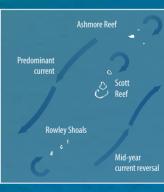
Larval Connectivity

Spawning corals, such as *Acropora tenuis*, release eggs and sperm which are fertilised and develop in the water column. They spend days to weeks drifting with the currents until they are ready to settle, usually less than twenty kilometres from their parent colony.





Scott Reef and its neighbours are extremely isolated. Moving between these reef systems is a long journey for both coral and fish larvae, which must travel for weeks on ocean currents over hundreds of kilometres. Scientists concluded that few larvae disperse successfully among these oceanic reef systems, with most settling on their home reef.



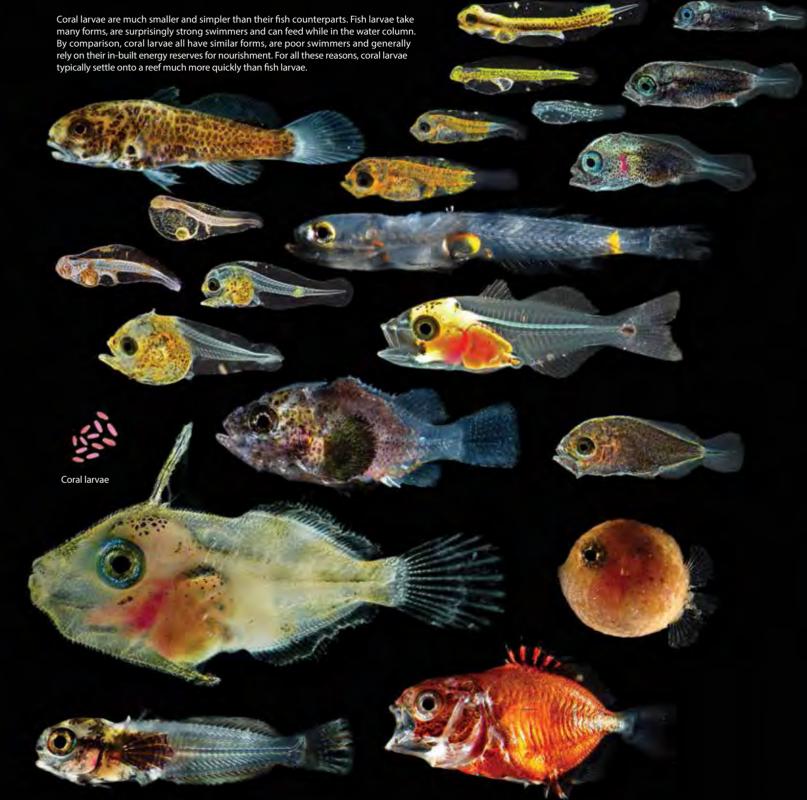
Going with the flow

The likelihood of coral larvae from Scott Reef reaching one of the neighbouring reef systems depends upon the speed and direction of the currents in the surrounding oceans, and upon how long the larvae can survive before settling. Until recently, neither of these factors was well known.

To study the currents, scientists used satellite-tracked drifters, devices that they released from one reef system and tracked as they flowed towards other reef systems. In more recent years, they have also used ocean models to predict current movements over a much broader range of environmental conditions.

These studies have shown that during the calm conditions that characterise periods of coral spawning, prevailing currents can retain coral larvae within a reef system for days to weeks. Once in the open ocean, dispersal times between the reef systems are in the order of one to two months. Interestingly, in the middle of the year the currents switch direction, from a predominantly southward flow in autumn to a northward flow in spring.





The long journey

Once researchers had estimates of how long it might take coral and fish larvae to travel between reefs, they could contemplate the related question of whether larvae live long enough to make such a journey.

The larval competency period – the time taken before larvae are ready to settle – varies widely for different species. Among corals, most brooded larvae are ready to settle when released from the parent, and usually do so within hours. For spawning corals, which are the majority, larvae need at least a few days drifting in the water column before they are ready to attach themselves to the reef. This minimum competency period is also affected by the conditions in the water, such as its temperature, so can vary substantially between regions. To estimate natural rates of larval development at Scott Reef, scientists used nets to capture thousands of embryos and larvae following a spawning event in 2003, and simultaneously conducted settlement experiments in aquaria.

The results showed that coral larvae at Scott Reef were ready to settle and attach to the reef within three days of spawning, sooner than had been documented in earlier experiments at other reefs. This difference of just a few days can have important implications for the dispersal distances of larvae, particularly because it can mean the difference between remaining on the reef and being carried into the open ocean.

Fish larvae, unlike their coral counterparts, have longer dispersal times that can extend from weeks to months. They are also able to swim and sense the reef environment around them far better than coral larvae, meaning they have some control over the distance and direction that they travel, particularly when ready to settle. Fortunately for scientists, they also have an in-built recorder of the period they spend in the larval stage. To determine how long fish larvae remain in the water column, scientists analyse the fishes' ear bones, called 'otoliths'. These bones contain rings – similar to tree rings – that are laid down each day, and display a distinct signal when the larvae settle at their new patch of reef.

In 2010, researchers painstakingly measured increments on the tiny otoliths from hundreds of juveniles of two common fish species (*Chromis margaritifer* and *Cheilodipterus artus*) from Scott Reef. The results suggested that the larval fishes remained in the plankton for between 25 and 45 days before settling. Based on this planktonic larval duration and current speeds, they calculated that larvae could theoretically disperse between Scott Reef and the other reef systems.



As with the growth rings of a tree trunk, the ear bones (otoliths) of juvenile fishes record the time they have spent in the water column before settling on the reef. Each fine increment represents a day in their life, and these are counted up to the settlement mark, which is notably thicker.

Leaving home

Travelling through the open ocean is perilous for larvae. A huge variety of animals are eager to consume them, particularly as they approach a reef where the number of potential predators increases dramatically. Therefore, it is not enough to know that larvae theoretically could reach other reefs in the region, it is necessary to know whether they actually survive the journey in sufficient numbers to contribute to their new populations.

Directly tracking billions of tiny larvae through hundreds of kilometres of ocean to determine their destination is impossible, so researchers must infer this information from a range of indirect methods. In addition to the inferences based on current speeds and larval durations, the relationship between the number of adult individuals and the number of new coral recruits on a reef can also provide insights into larval connectivity.

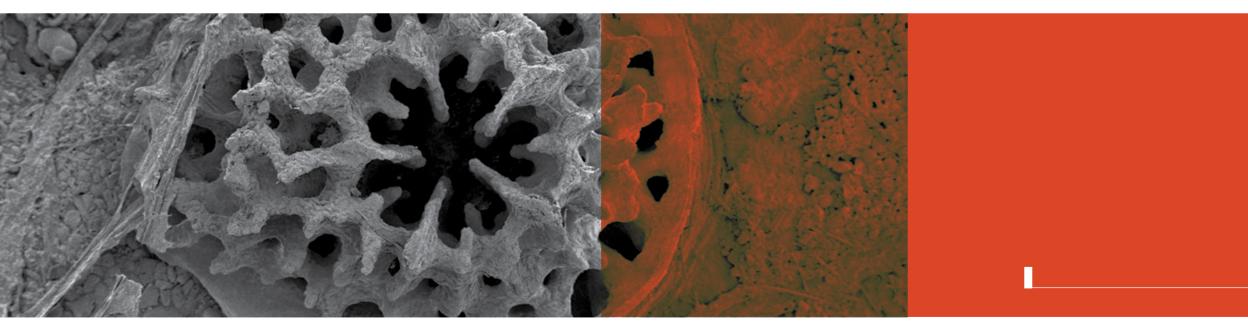
A powerful example of this approach emerged at Scott Reef, after the mass bleaching event in 1998 killed around 80 per cent of the corals. In the five years after the bleaching event, rates of coral recruitment were less than six per cent of those before the disturbance. However, over the following decade the number of new recruits increased proportionally to the number of adult corals, providing clear evidence that recovery depended on the survivors and was not aided by a supply of larvae from the neighbouring reef systems.

More recently, advances in genetic analyses have provided another way to examine larval connectivity among reef systems. In the first study of its kind in Western Australia, researchers examined the genetic identity of thousands of samples collected from two species of coral (*Acropora tenuis* and *Seriatopora hystrix*) and fish (*Chromis margaritifer* and *Cheilodipterus artus*). The genetic similarity among samples taken from different locations at Scott Reef and the Rowley Shoals allowed scientists to estimate larval connectivity within and among these reef systems. The results supported those obtained from the other methods, suggesting that the brooding coral typically disperses over distances of a few kilometres and the spawning coral over distances of less than 20 kilometres; as expected, the fishes dispersed over larger distances, typically among the reefs within each of the systems. However, there was little evidence of significant larval exchange between the two reef systems for either the corals or the fishes.

What's born on the reef, stays on the reef

Researchers at Scott Reef have taken a unique approach by combining a range of complementary methods to answer the complex question of larval connectivity. Combining oceanography with studies of larval development, stock-recruitment and genetics has led to the conclusion that the coral and fish communities at Scott Reef produce most of the larvae that replenish populations at this isolated location. There is little evidence of a large and regular supply of larvae from the other reef systems in the region.

In other words, when it comes to recovering from disturbances, Scott Reef and the other reef systems in the region are largely on their own. Without an external supply of recruits, communities may take longer to recover from severe, widespread disturbances than they would otherwise. Severe or repeated disturbances could also affect the persistence of susceptible species, potentially eradicating such populations from Scott Reef, with little hope for replenishment from external sources.



Coral Recruitment

After drifting in the water column, coral larvae attach themselves to the reef's surface and metamorphose into a single coral polyp. The new coral continues to divide and grow, competing for space against already-established organisms, including other corals, sponges and algae. After drifting perilously through the water column, coral larvae face their next challenge – finding a suitable spot to attach to the reef, metamorphose, and grow into a young coral. No event in the lifetime of the coral will be more important than where it settles, as it will remain in that place for the rest of its life. This process – known as recruitment – is critical to maintaining populations by replacing the corals that have died. Researchers working at Scott Reef have long recognised the importance of this process to the reef, and in 1995 began one of the longest-running studies of coral recruitment on record. Tens of thousands of coral recruits have since been counted and identified, providing a unique insight into how recruitment varies according to the abundance of adult corals and the exposure of Scott Reef to varying disturbances.

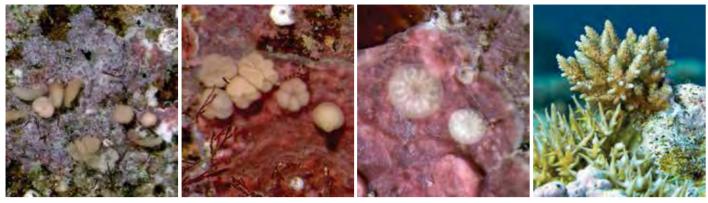
Settling down

Successful recruitment relies on the coral completing its larval stage, attaching to the reef and metamorphosing into a polyp, where it begins life as a coral colony.

Coral larvae are just one millimetre in length when they begin the process of settling. They can detect chemical cues that attract them to a patch of reef, and then spend some time searching the reef surface for a suitable site of attachment. Larvae most commonly attach to hard surfaces, coated in pink coralline algae and other microscopic biofilms, often showing preference for holes or crevices in the reef. The choice of settlement site at this early stage influences the survival of the coral through its entire life, as moving is not an option.

Once attached to the reef, a larva begins the process of metamorphosis. Within a day, it transforms from a sausage shape into a flattened disc, on which developing tentacles and a mouth are visible. Over the following days, the mouth and tentacles fully develop and the polyp secretes a calcium carbonate skeleton. This primary polyp divides to create another, these in turn divide, and the process continues, eventually producing a coral colony that may contain many thousands of polyps.

The tiny coral is particularly vulnerable in this early stage of its life. The colony is less than a few centimetres in size during its first year. At this age, it can easily be overgrown by other organisms, such as algae, sponges or even other corals. It can also be buried under sediment or rubble, or consumed by fishes scraping away at the reef while feeding.



Coral larvae respond to chemical cues while searching the reef surface. When selecting a suitable place to attach, they often prefer certain species of red coralline algae. After attaching, the larva metamorphoses and begin to form a mouth, tentacles and a skeleton. The single coral polyp then begins to divide, and the colony may eventually contain many thousands of polyps.

How many coral recruits?

Measuring coral recruitment provides important information about the health and resilience of a reef. High numbers of new coral recruits at a reef suggest it is receiving an adequate supply of coral larvae to sustain coral populations and predicts faster recovery from disturbances. In contrast, consistently low numbers of coral recruits suggest an unhealthy reef with coral communities that will decline in the future.

Counting the number of new corals on reef is, however, no easy task. Recruitment can be patchy and is influenced by a wide range of factors that researchers do not yet fully understand. For example, the number of new corals depends on the amount of available space – there may be more coral recruits on a patch of reef covered in coralline algae than on a patch densely covered by macroalgae, so estimates must account for these variables. Another challenge for scientists attempting to measure recruitment is the tiny size of the new corals – they are barely visible to the naked eye and can be extremely hard to find on the reef, especially given their preference for settling in small holes and crevices.

The researchers' solution to the problem of measuring coral recruitment is to provide the larvae with an alternative settlement surface, of a standard size and structure, that can be easily attached to the reef and then collected with the recruits attached. These 'settlement plates' are deployed approximately one month before coral spawning, during which time they become covered in the coralline algae and associated biofilms on which larvae prefer to settle. A month after spawning, the settlement plates are retrieved, and the tiny coral skeletons counted and identified under a microscope.

Opposite page: Researchers use settlement plates to measure the number of corals recruiting to a community. When first deployed, these terracotta plates are clean, but quickly become covered in the biofilms and the red coralline algae on which coral prefer to settle.



Recruitment in space and time

Across Scott Reef, scientists discovered that the number of coral recruits in shallow waters varied according to the number of adult corals – an extremely important finding that indicates recovery from disturbances at Scott Reef is not aided by a large supply of larvae from other reefs. This relationship was established after the 1998 mass bleaching event, when the number of recruits dropped to nearly zero following a comparable decline in adults. Monitoring over the following decade showed that the number of recruits remained low for several years, only returning to previous levels after the number of reproductive corals had also recovered.

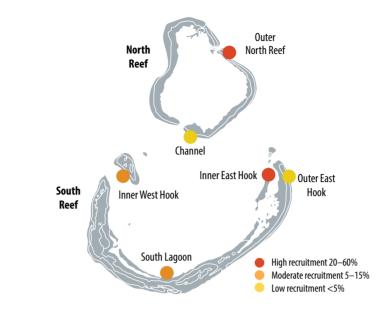
The relationship between the number of adults and recruits also applied to much smaller areas of the reef for the brooding corals. This is understandable because their larvae are fully developed when released and typically disperse over distances of less than a few kilometres – unlike spawning corals, whose larvae develop in the water column and can disperse over greater distances. Recruitment in the spawning corals varied considerably among locations, with certain areas showing either consistently high or low recruitment. This supports other research suggesting that the larvae of spawning corals can travel among locations separated by around 10 to 20 kilometres, and that the direction of dispersal is influenced by the prevailing currents. Thus, scientists were able to identify locations at Scott Reef that are sources, and sinks, of larval recruitment – information that is critical for managing the reef through disturbances.

Deep recruitment

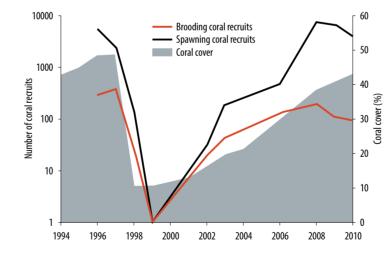
Much of the knowledge about coral recruitment at Scott Reef has come from the shallow reefs. However, the discovery of the extensive coral communities in the deep lagoon at South Reef led researchers to guestion whether reproduction and recruitment there display similar patterns to those seen in the shallows. Since divers cannot safely access the deep lagoon, settlement plates were attached to instrument frames lowered to the sea floor. Preliminary findings identified a peak in coral recruitment at the same time as the coral spawning in the shallows, suggesting similarities in reproduction between the shallow and deep water corals.

There were, however, some notable differences between the settlement plates deployed in the shallow and deep water. For example, recruits in the shallow water areas commonly settled on the underside of the tiles, whereas in the deep a much higher proportion settled on the upper surface, probably in response to the low light levels in the deep. Additionally, by far the highest number of recruits in the shallows belonged to a single coral genus, the Acropora. By comparison, there were far fewer Acropora recruits in the deep, which is reflected in the significantly lower adult numbers of these corals at these depths.

These initial findings provide some information about patterns of reproduction and recruitment in the deep water corals, but there is still much to learn about these newly discovered communities.

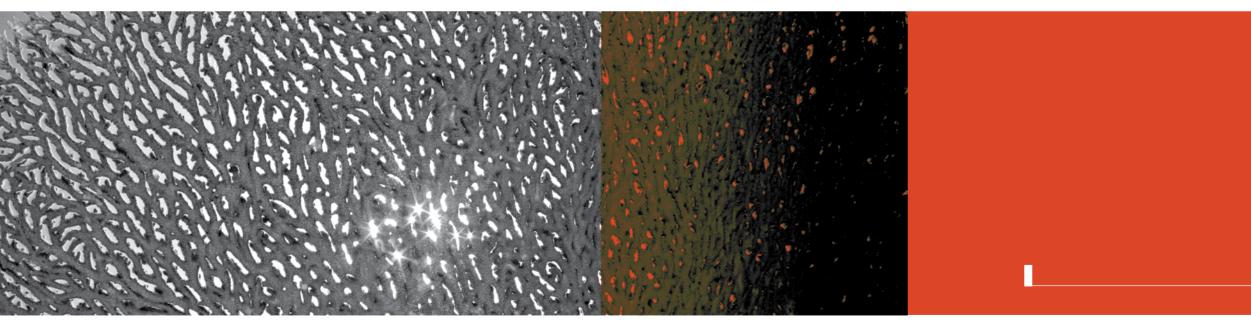


In addition to the abundance of adult corals at different locations, the rates of recruitment at Scott Reef are influenced by the direction of currents. Some locations, such as Inner East Hook, have consistently high rates of recruitment because eddying currents trap larvae: these locations are recruitment 'sinks'. Just a few kilometres away at Outer East Hook, consistently low recruitment is caused by currents carrying larvae away: these locations are 'sources' of recruitment.

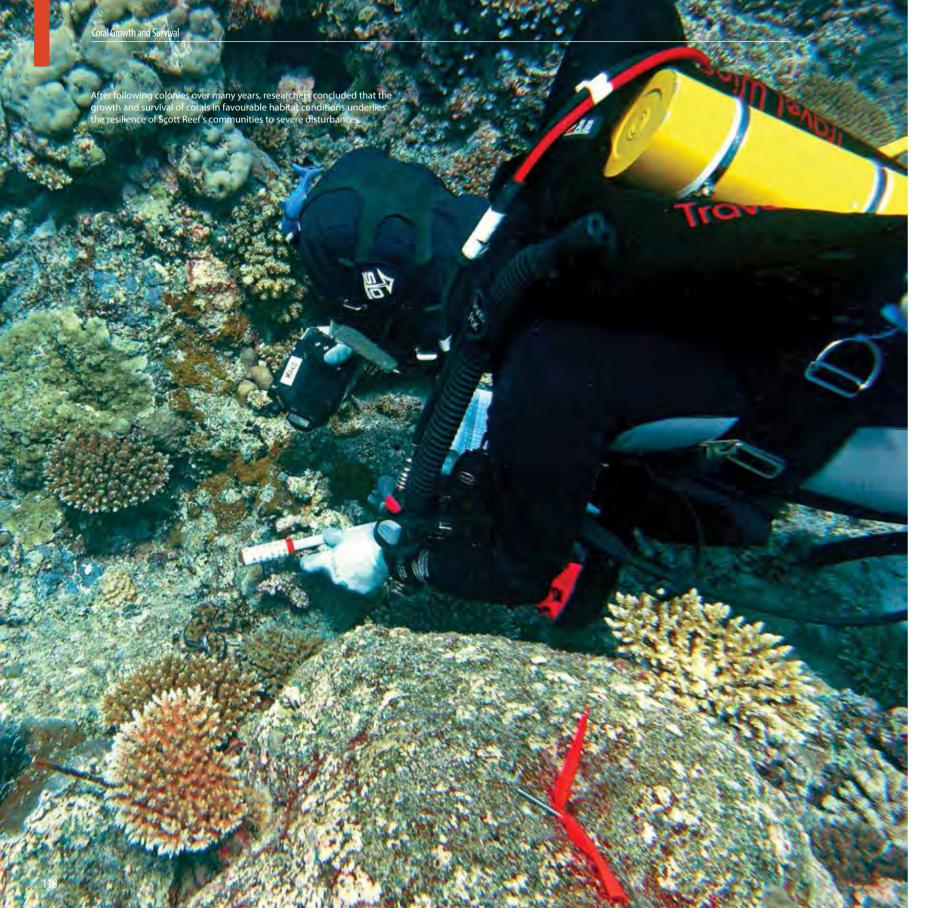


At Scott Reef, there was a strong correlation between the rates of recruitment of spawning and brooding corals and the changes in coral cover before and after the mass coral bleaching. This finding has important implications for the reef, providing clear evidence that its recovery from disturbances primarily relies on the survivors, rather than being aided by the supply of larvae from other reefs in the region.





Coral Growth and Survival



The isolation of Scott Reef has offered a rare opportunity to study the different factors influencing the recovery of coral communities from catastrophic disturbances. Although the reef's recovery is not aided by many recruits from other distant reefs in the region, it does benefit from the absence of many chronic pressures that affect reefs closer to the mainland, such as poor water quality and declining numbers of herbivorous fishes. Research at Scott Reef has revealed some new insights regarding the crucial role of growth and survival of new recruits in maintaining coral communities on isolated reefs — information that will assist in developing management strategies to maximise the reef's resilience to emerging disturbances acting on a global scale.

Understanding growth and survival

The capacity of a coral reef to withstand disturbances depends on the rates of growth and survival of the different coral colonies that make up the communities. In many places around the world this capacity has been compromised by a combination of human and natural disturbances that have resulted in long-term degradation.

To prevent and remedy these problems, it is important to not only describe the degradation of coral communities, but to fully understand why they occur. This approach includes quantifying the effects of pressures on the growth and survival of different stages of the coral's life cycle, in order to make predictions about how communities will respond to these pressures.

Existing studies have gone some way to clarifying these issues. For example, researchers know that table corals have faster growth but lower survival than those with a massive growth form. Growth and survival also tend to vary among different colony sizes within a coral species, so that the smallest colonies typically have much lower rates of survival than larger colonies.

However, many studies to date have been conducted on nearshore reefs or those under chronic stress – very different habitat conditions to those at Scott Reef and similar offshore reef systems.



Almost 6000 colonies of massive and table corals, across a range of size classes, were tagged and resurveyed over several years to measure rates of growth and survival. Tagged colonies included the table *Acropora* and massive *Goniastrea* corals, which are among the most abundant corals at Scott Reef. Many colonies were less than one centimetre in diameter, and finding these tiny corals among all the other organisms on the reef presented scientists with a considerable challenge.

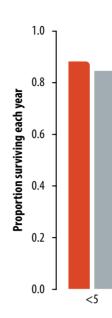
Interpreting changes

Between 2006 and 2010, researchers at Scott Reef measured annual rates of growth and survival for thousands of colonies of *Acropora spicifera* and *Goniastrea* spp. (*G. edwardsi* and *G. retiformis*) at several locations. These species were chosen because they are typical of the most common table and massive corals at the reef.

As expected, these studies revealed large variations in the rates of growth between the table and massive corals. Without major disturbances, the table coral *A. spicifera* increased in diameter by between two and nine centimetres each year, much faster than the massive *Goniastrea* corals, which generally grew less than one centimetre each year. Unexpectedly, however, there was little difference in survival, which averaged over 90 per cent per year for both groups of coral.

Table corals were, however, more susceptible than massive corals to the disturbances that affected the reef. After cyclone George struck in 2007, the growth and survival of table corals was reduced for several months at the most exposed locations. In those parts of the reef, survival rates were especially low among the largest colonies because they were most likely to be toppled over or fragmented by the powerful waves, which had comparatively little effect on the smallest colonies.

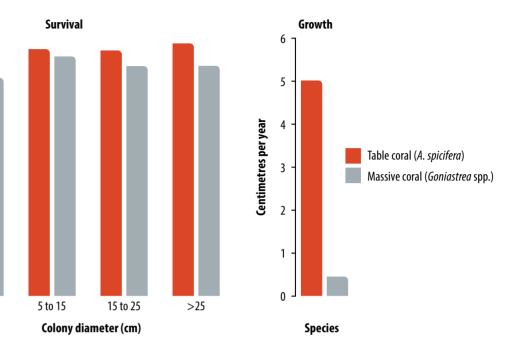
Some of the demographic research at Scott Reef produced more unexpected results. In both of the coral groups, there were only small differences in survival rates among the different colony size classes, which were consistently above 80 per cent per year from 2008 to 2010. Significantly, the smallest colonies had similar survival rates to the largest colonies, much higher than those often reported for other reefs.



In the absence of major disturbances, the corals at Scott Reef have high rates of survival, particularly the smaller colonies. From 2008 to 2010, the survival rates of all size classes of *Acropora spicifera* and *Goniastrea* spp. were consistently above 80 per cent per year. A disease outbreak and a moderate bleaching event in 2010 had little effect on their survival. However, growth rates varied considerably between the coral groups, with the table coral *A. spicifera* growing much faster than the massive *Goniastrea* spp.



Many of the *Acropora spicifera* colonies that were originally tagged in 2006 were still alive four years later, having grown from small juveniles into large adult colonies. For example, colony 'SL1-579' was only a few centimetres across when first tagged in 2006, but had grown to over 20 centimetres in diameter by 2010.



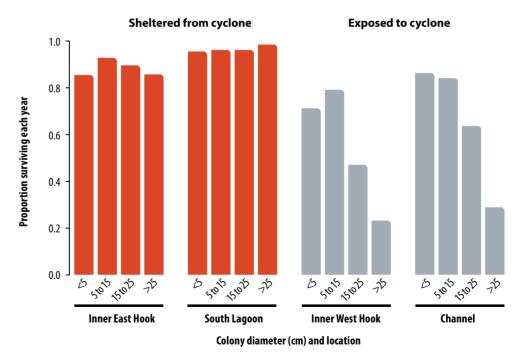
Favourable conditions at Scott Reef allowed coral communities to change from low cover and diversity following the mass bleaching in 1998, to high cover and diversity a decade later. A reef surface suitable for coral recruits, low algal cover and an abundance of herbivorous fishes, along with clear water, helped the corals to survive and grow.

Recovery from disturbances

The high growth and survival of corals at Scott Reef were particularly important to its recovery following the devastating mass bleaching in 1998. The destruction that occurred during this event was so severe that it affected all groups and sizes of coral colonies. The death of corals and the corresponding reductions in recruitment had long-lasting implications for the recovery of communities.

However, the high water temperatures that caused the mass bleaching persisted for only a few months, after which conditions returned to normal. The favourable conditions that were more typical at Scott Reef helped to ensure high rates of growth and survival during the recovery period. Those conditions included suitable space for recruitment, a low abundance of competing corals or macroalgae, a high abundance of herbivorous fishes and good water guality. Indeed, population models for the table corals from 2008 to 2010 indicated that the size of several populations increased by 20 per cent per year, suggesting they could double in size in less than five years. Consequently, the corals that survived the mass bleaching and the offspring they produced thrived in the favourable conditions, and communities had largely recovered from the coral bleaching within 12 years, much faster than initially predicted.

This illustrates how resilient coral reefs can be to periodic disturbances – even isolated coral reefs, such as Scott Reef, that do not receive a large supply of recruits from outside – provided local conditions remain favourable.



killed instantly, while others died from their injuries over the following year.

In areas exposed to cyclone George in 2007, survival of Acropora spicifera was much lower. The largest colonies were the worst affected by the cyclonic waves, some being