Left: Coral reef fish often live in complex social groups controlled by stress due to aggression by larger fish.

Distress a Normal Part of Life for a Damsel

The stress of being around too many other females causes pregnant female fish to have smaller babies. Mark McCormick discusses implications for reef resilience.

The first thing we notice when we go snorkelling or diving on a coral reef is the thousands of fish of many types that inhabit these complex ecosystems. In part, it is stress that enables so many fish to live together.

Most small coral reef fish live in tight social systems with well-defined ecological roles. These social systems usually involve a dominance hierarchy that is based on size. Bigger fish are aggressive to smaller fish, and it is the stress associated with these interactions that can prevent subordinate fish from outgrowing or out-competing the dominants. Bigger is usually better on the reef.

While stress keeps things in order around the reef, the physiological machinery that comes with stressful situations – the butterflies in our stomach or our racing heart – can have adverse effects. Aquarists find that too much stress, such as when salmon are stocked at too high a density in a cage, may lead to reproductive shutdown.

Work on temperate snapper (*Pagrus auratus*), has shown that fish caught on a hook and line and then released can be so stressed that they may stop putting energy into reproduction; moreover females may even reabsorb the eggs that were ready to be spawned that season. Fortunately, normal life on a coral reef does not usually reach these extremes for most of its inhabitants.

Recent research at James Cook University's ARC Centre of Excellence for Coral Reef Studies has shown that the more fish that a breeding damselfish interacts with when it is developing its eggs, the higher the mother's level of stress and the smaller its offspring. The clear tropical waters around the Lizard Island Research Station allowed us to change the number of females who could interact with mothers on the reef and look at how it influenced the characteristics of the larvae produced.

These damselfish are small and may live their whole life in a patch of reef the size of a garden shed. This means we can come back to the same spots and find exactly the same fish. By catching some fish, and releasing others, we can change the numbers of fish that a breeding female will interact with.

Hours of underwater observations show that some feisty females spend up to 88% of their time displaying and chasing other fish. All this chasing about causes stress for mothers, and for the fish they chase.

Ambon damselfish lay benthic eggs that develop rapidly. All developmental rhythms, such as the beating of their heart, are faster in embryos from stressed mothers.

Smaller larvae are produced due to a stress response that leads to increased levels of the hormone cortisol. Humans also have cortisol, which is produced in stressful situations. Cortisol in the blood of the mother damselfish is taken up by the eggs during their formation. Cortisol plays many roles in fish, but during early development it speeds up developmental rhythms.

From the first cleavage of the fertilised egg, the developing embryo has rhythmical pulsations. With the formation of the myotomal muscle blocks about 1 day after fertilisation, the body flicks faster in larvae exposed to higher levels of cortisol. When the heart forms after 32 hours, the heart beats faster in larvae produced by stressed mums. All this activity leaves less energy available to put into growth, and leads to the production of smaller babies.

So why do we need to know this? Well, these larvae are the start of the next generation on the reef. Larvae are released from parents on the reef to come back looking like small fish 2–3 weeks later. While many millions are released, very few will survive to return to the adult habitat. Death is almost a certainty.

However, all larvae are not created equal. Research at James Cook University and elsewhere has shown that even small differences in size can make large differences in performance. Larger larvae swim faster, find food more efficiently and are better at avoiding or escaping predators.

The initial advantages of being large are amplified by faster growth rates – what is known as the "silver spoon" effect. As larvae get older, the range in size, as well as other body features, increases within the group of larvae spawned at the same time. We get "shooters", "runts" and everything in between.

Our research has shown that larvae that eat more and grow faster typically have better survival. A study we recently conducted on a tropical surgeonfish showed that fish that grew faster soon after they had used up their yolk reserves contributed most to the next generation.

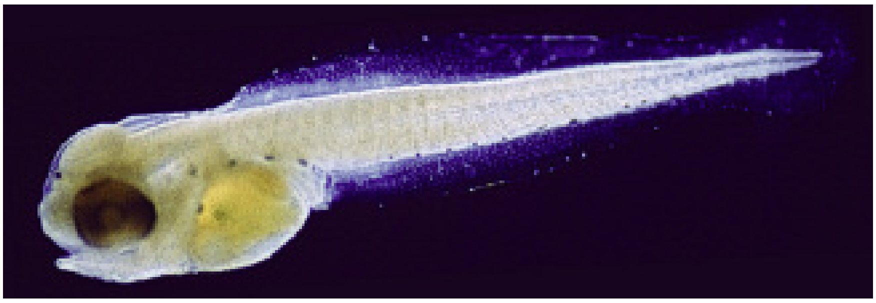
The advantages of a privileged birth don't stop upon returning to the reef. At the end of their larval phase the little larvae have grown into small fish and they must come back to a reef or die.

The predators on the reef are much different from the tuna, mackerel and jellyfish that they have avoided up until now. Larvae face a wall of hungry mouths as they try and find a suitable habitat to make their home.

The most voracious are the bottom-dwelling lizardfish, small rock cods and dottybacks. The juvenile fish are naïve to the ways of the reef and don't yet know the identity of their enemies, so at least half will be eaten within the first 5 days on the reef.

Just as larval survival is tied to the health of their mother when she was pregnant, so she influences who survives after settlement on the reef. Juvenile survival is closely tied to how fat they got and how quickly they grew during the larval phase. Following the fate of newly settled fish that were individually tagged underwater shows that being even 1 mm larger than their neighbour can mean a better chance of survival.

A recent study by another of the ARC Centre's chief investigators, Dr Mark Meekan, on a north-western Australian damselfish showed that whether a fish survived the first 3 months of juvenile life could be



Ambon damselfish larvae hatch from an egg after 4–5 days to start a 2-week larval phase, during which most die. Although only 3 mm long, their large eyes and mouth allow them to capture food almost immediately. While they learn to feed they survive on the nutrients carried in their yolk-sac.

Juveniles, shown here with a characteristic eye-spot on the dorsal fin, suffer high mortality. Survival of larvae and juveniles is greatly influenced by the characteristics of their mothers.

traced back to the characteristics of the larvae at hatching: once again, the flow-on benefits of a privileged birth. All of this research shows that mothers do matter.

Although research on the flow-on effects of maternal stress to larvae has only been conducted on the Ambon damselfish (*Pomacentrus amboinensis*), it is likely that many species may show this mechanism. All modern bony fish have broadly similar physiologies. Stress will cause elevations in cortisol, which may be included in the eggs during their production. Likewise, cortisol is also likely to have similar influences on the development of embryos in many fish groups. So, in many fish species, mothers subjected to high stress are likely to produce smaller offspring that perform poorly.

There are broader implications of this research. The amount of stress that a mother fish has is not only derived from behavioural interactions with other females or predators. Sampling of mothers from different reef habitats shows that levels of stress are related to habitat.

With a changing climate, reef habitats are also experiencing change. These changes can cause direct death to its inhabitants, as a habitat changes from one type to another, such as a change from live coral to algal-covered coral rubble. To date, researchers have focused on this sort of direct change in community composition. The indirect, or sub-lethal, effects of a changing reef to a coral reef fish community have not yet been explored.

Those fish that survive changes in the nature of their living space may be more stressed, and this may influence the quality of the offspring they produce. The consequences of environmental change may be a lower proportion of the larvae surviving the larval phase to repopulate our reefs.

However, the take-home messages are not all dire. The same physiology that leads to small larvae from stressed mothers also leads to larger, fitter offspring being produced by unstressed mums. For the Ambon damselfish, mothers are least stressed when at low densities – and this is when they produce the largest larvae. This suggests that when populations are low they may be able to produce larvae that have higher performance and a higher chance of surviving to replenish the reefs. This may mean they have higher resilience than expected at low densities.

While small and unassuming, the Ambon damselfish has played an important role in our understanding of the factors that influence the dynamics of fish populations on coral reefs. Research continues to explore the link between the parents, the survival of their offspring and whether the "silver spoon effect" extends through to reproductive success in the next generation.

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Big Picture from Small Fish

What influences where fish live and how many there are? These are simple questions that fish biologists around the world spend most of their time investigating. The answers are complex and of fundamental importance to population biologists, resource managers and conservationists.

Since commercially important species, such as coral trout, are of most economic value, we tend to imagine that most research would focus on these species. Unfortunately, the same features that make trout attractive to fishers make them difficult to study. They are large in size, roam widely across the reef and are relatively uncommon. This makes them very difficult to study.

To understand the processes that underlie fluctuations in the number of fish on a reef, we must look to smaller species. These are chosen so that they have most of the same life history features of our coral trout. Similarities include a sex-changing adult phase, a larval phase of about 3 weeks followed by a site-attached juvenile phase.

Researchers call these "model species", and study them in the hope that the details we learn about their life cycle will be relevant to our commercial species. While our models would be at home in Nemo's fish tank, most of what we understand about how and why fish populations fluctuate comes from these small, brightly coloured fish.