Surf, Turf, and Eggs

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For most southern Californians, spring is marked by warming air, blooming golden poppies, the return of swallows to the San Juan Capistrano breeding rounds, and opening day at Dodger stadium. For much of southern California's diving community, however, it is marked by the beginning of mating season of California's state marine fish.

The frenzy begins in mid-March, when the observant diver exploring shallow rocky reefs will notice male Garibaldi working over what appears to be just another section of boulder encrusted with the usual assortment of bryozoans, tunicates, brown algae, and debris. The male works as if he just downed a double espresso, performing a series of intense bites on the nearby rocky surface to remove debris, followed by a "fan" in which he rubs his tail and anal fin against the boulder in a rapid sweeping motion.

When divers return to these same areas about a month later, they will find boulders covered with round carpets of red filamentous algae, some of them as large as truck tires. They will also notice that the guardians of these carpets have become increasingly belligerent--divers that approach too closely often find a foot long fish clamped onto their lip or cheek. If they wait patiently enough, they will see the bright orange fish swimming acrobatic loops accompanied by grunting sounds--a behavior called "dipping." With a little luck, they may also witness a passing female swim into the nest of a dipping male--the



The Garibaldi are among the many aquatic fauna that thrive around California's lush coastal kelp forests.

ritual has begun.

The Garibaldi, or ocean goldfish (*Hypsypops rubicundus*), is the largest member of the damselfish family (Pomacentridae). The flaming orange-red Garibaldi gets its name from the Italian leader Giuseppe Garibaldi, whose famed army wore flashy red shirts. Most of the 240 or so members of this family are less than eight inches long and are found on tropical reefs of the Pacific, Atlantic, and Indian Oceans, and also in many home aquaria. But not only is the Garibaldi, at about 12 inches long, the largest member of this family--it is one of the few species that has invaded temperate marine waters, ranging from Monterey South to central Baja.

Juvenile Garibaldi that have just settled onto the rocky reefs are bright orange with iridescent blue spots. As they age, they lost the blue spots while the orange gets brighter. As adults, both males and females are a brilliant orange and are indistinguishable except by behavior.

As in other members of this family (and in many other fishes), it is the male that builds the nest, and, if

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he is lucky enough to attract females, takes care of the eggs until they hatch and enter the plankton as tiny larval fish. And, in most bony fishes, Garibaldi eggs are fertilized externally, with the male squirting spermatozoa on the eggs after they have been released by the female. When Garibaldi eggs are first laid, they are bright yellow and extremely conspicuous against the maroon algal mat. As they age, they gradually turn to gray, and then to silver before hatching in about two weeks. While most other damselfish simply clean off a rock or piece of coral to use as a nest, male Garibaldi spend about a month culturing their algal carpet each spawning season. Moreover, they culture a new carpet on the same spot on the same rock every year of their reproductive lives, which may last more than ten years. Spawning begins in late April and continues for about four months. The nesting and spawning activity is so conspicuous that fish-watchers and photographers can be guaranteed to observe nests and guardian males in less than 20 feet of water, and are often fortunate enough to witness spawning itself.

As an avid snorkeler growing up in southern California, I spent hours every spring and summer watching the Garibaldi perform their annual ritual in the clear waters off Santa Catalina Island, Laguna Beach, and La Jolla. So, when it came time to choose a project for my doctoral research at Oregon State University, Garibaldi seemed like an obvious choice. I returned to Big Fisherman Cove on Santa Catalina's leeward side and began what has become a ten-year study on the reproductive behavior of the world's largest damselfish.

Recalling that only a small fraction of nests I observed actually had eggs and that males were usually unsuccessful in their courtship efforts, I was most interested in how females select among the multitude of suitors. My efforts to understand the process of mate choice in Garibaldi taught me two things: Females are picky and the Rich get richer.

Picky Females

One of the conveniences of studying this species proved to be that females searching for males are very conspicuous, swimming in an erratic fashion with all fins erect. Thus, I could follow these females and observe them as they visited prospective mates. However, one of the inconveniences turned out to be that females seemed to spend an eternity making up their minds. I usually had to follow a female for at least an hour before she spawned and I followed one female for five hours. Females shuttled back and forth between their home territory and the nests of males, rejecting what seemed to me to be perfectly good nests and males, while I became numb from the cold water and sometimes dangerously low on air. After a complete season, it became clear to me that when females finally did spawn, it was nearly always with a male who already had eggs in his nest--but not only were females showing a strong preference for males with eggs, the eggs had to be yellow, a sign that they were fresh.

The Rich Get Richer

While my observations were suggestive, experiments were needed to confirm that the eggs themselves indeed make a difference. Like any good scientist, I sought a hi-tech solution to my problem. During the next spawning season, I returned to Big Fisherman Cover armed with mascara combs and proceeded to remove eggs from nests that contained fresh yellow eggs. In some cases, I left a patch of eggs in the nest. In an equal number of others, I left no eggs. While this did little to win the affection of the guardian males, it did help answer my question--males with some yellow eggs were more likely to receive additional eggs than the nests with old eggs.

I was reasonably satisfied that the presence of fresh young eggs did in fact influence a female's choice of spawning partner. But, as usual, answering one question begs at least one more. The most obvious question was "How do females benefit by choosing males with young eggs?" I soon discovered that males are also sensitive to the number of eggs they have in their nests and adjust their level of parental care accordingly. For instance, if a male received a clutch of eggs, he would eat the entire clutch if he failed to receive more eggs within several days. In fact, a male would cannibalize these "lone" clutches at precisely the age at which they were no longer attractive to females. Moreover, when I manipulated the number of eggs in male nests, males with more eggs were also more aggressive in their defense of the nest. So, the best way for a female to avoid the risk of having her eggs become a lone clutch, and thus be eaten by the male, is to deposit her eggs with other eggs. This also increases the chances that her clutch will be part of a larger brood that will receive more care.

But why does the female care about the age of eggs in a male's nest as well as the number? If a female deposits her eggs in a nest of older eggs, those eggs will soon hatch, leaving her eggs as a lone

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clutch. I found that if a female deposited her eggs as the last clutch in a nest with mostly older eggs, she was much more likely to have her eggs cannibalized or neglected by the male than if the eggs were deposited in a nest dominated by younger eggs.

To Care or Not to Care...

It seems that the benefit to females of laying in nests with young eggs hinges on how the number and stage of eggs affect male parental investment. Why should this matter to a male? Shouldn't a male invest all he can if in his precious offspring? Simply put: No. To understand this we have to understand what a male gains and loses by caring for his offspring--the costs and benefits.

As any parent knows, taking care of offspring is hard work. When males care for eggs, they increase the amount of energy they expend: They most fan the eggs to keep them supplied with oxygen and chase away intruders that want to feed on the tasty embryos. And because they have to be near the nest so much, they are unable to feed as much as they otherwise would. So, taking care of eggs has a high cost--males expend more energy than they take in and thus lose weight and become weakened. This can lead to all sorts of undesirable consequences that may compromise the male's ability to mate in the future. These include decreased growth, increased susceptibility to disease, and a decreased ability to fend off stronger males that may want the nest for themselves.

To make up for these costs, males require a large benefit--namely, a large number of eggs. Because the benefit in eggs hatched is much higher for a larger brood than a smaller brood, males are willing to pay a higher cost by expending more effort on the care of larger broods. Very small broods may not yield enough benefit to warrant the cost. At the extreme, a male may decide to avoid caring for such a brood by eating it. Not only does this enable him to get out of rearing a brood that isn't worth the cost, but he actually gains some energy at the female's expense. This energy can be invested in future, hopefully larger, broods that will yield a higher benefit.

Eating one's own offspring has been termed filial cannibalism and is very common in fishes and even some salamanders. It is part of a more general phenomenon called infanticide--the killing of viable offspring--which occurs in virtually every animal that provides parental care, including humans and other primates.

Big Men of the Cove

So, for reasons that make sense when we consider the costs and benefits to males of caring for offspring, once a male receives an initial clutch of eggs, he becomes a big man of the cove (BMOC). In fact, I often observed several females in queue waiting to deposit their eggs in nests with young eggs. Meanwhile, males without eggs were desperately attempting to lure females into their nest. But how does a male get on the track to being a BMOC? How does he get that first clutch that usually sends him into a spawning frenzy? While females clearly prefer nests with young eggs, they must sometimes spawn in empty nests when males with eggs are not available or have no space in their nest. Clearly, from a male's point of view, getting that first clutch is the single most important event of the season.

It was an obvious first step to wonder if the appearance of male Garibaldi' unusual algal mats influenced which males succeeded in attracting that first clutch. Garibaldi males may spend a month culturing the mat that sets them apart from their tropical relatives. Males remove unwanted green and brown algae, and continually crop the desirable red algae to about an inch in height. This is just like weeding and mowing a lawn. However, at any given time, some nests resemble well-manicured golfcourse greens while others resemble the field at RF. Stadium after a Skins game played in the rain. Could this difference influence female choice? Might females avoid spawning with males with sparse algal mats? To address this question, I measured the thickness of algal mats and compared their lushness with the number of days it took a male to receive his initial clutch. Indeed, the fewer bare or sparse patches in the nest, the sooner the male received eggs--voila! But, my bubble was burst when I discovered that the males with the sparse nests were also sluggish courters.

This quandary called for an even higher-tech solution. With the assistance of my helpful hardware man, I purchased the finest wire brush available (more than twice as expensive as the mascara combs). I then identified the finest nests in the cove and used my wire brush to shave down half of them, turning them into embarrassing shadows of their former selves. I disturbed the other half by waving

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the brush over them and similarly annoying the male. My expectation was that since all the males had been able to construct good nests and were good courters, they would all attract females to the nest where the females could then assess the thickness of the mat. If females preferred thick mats, they would be more likely to spawn in them after being attracted by a dipping male.

To my disappointment, the males didn't cooperate. While those males with high-quality nests continued to court vigorously, those whose nests had been shaved courted little. This presented a serious problem. Males seemed to be aware of their nest quality: Those with what appeared to be attractive nests courted much more than those whose nests were ruined. So, I couldn't tell if males with poor nests weren't getting eggs because their nests were poor or because they weren't courting as much.

Three things still worked in my favor. First, males couldn't or wouldn't abandon their nest if they didn't like it. Second, they couldn't build it quickly. Finally, the nests were large. What if a turned a large nest into two smaller nests--a thick one and a sparse one? With renewed enthusiasm and my wire brush, I identified 12 of the largest and thickest nests and proceeded to modify them. It worked. All nests eventually received eggs and the eggs were always deposited on the thicker half of the nest. Thus, it seems that females do prefer thicker nests and that males know this. Males with attractive nests court with confidence while those with unattractive nests waste little effort attracting females for what would ultimately be an unfruitful meeting.

But why does having a thick algal mat make a difference? After all, most self-respecting damsels are quite happy to place their eggs on bare rock. The answer to this question remains unknown but provides an excuse to return to the bountiful waters of southern California for seasons to come.

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