The sex lives of fishes

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In fishes as in all living beings, reproduction is the biggest game in town. The behavioral, anatomical, and physiological features that we see in fishes today are there because they were successfully passed on from generation to generation throughout the ages. They were passed on in the form of genes (bits of DNA) during the reproductive act. Those individuals that did not care about reproduction died without transmitting their genes to the next generation, and their contempt for the reproductive enterprise died with them. In contrast, those individuals that had an innate taste for mating propagated that trait through the population.

Evolutionarily speaking, stakes are very high in the reproductive game. There is pressure on all individuals to leave as many viable descendants as possible in the next generation. One way of doing this is to choose a sexual partner of high quality, one who will impart genetic value to the offspring, as well as taking good care of them. But for those individuals who score low in the mate choice game, there are other ways to pass on their genes, less flashy ways, tactics that are less straightforward, some might say less fair-play, but reasonably efficient nonetheless. These are the dirty little secrets of a fish's sex life.

Kleptogamy (sneaking)

In almost all fishes, fertilisation is external. The male's sperm and the female's eggs are released from the body and they must meet in open water for fertilisation to occur. While they float in water, a female's eggs are vulnerable to interception by the sperm of a male who may not be her chosen mate. Welcome to the world of kleptogamy, the stealing (*klepto*) of fertilisations (*gamy*) by an interloping male.[1]

Sometimes the cuckolding male is a territorial neighbour. After realising that a female is about to spawn next door, this neighbour tones down his bright nuptial colours (which would identify him as a territorial rival), becomes more female-like in appearance, and sneaks into the courting male's territory. When the female sheds her eggs, the sneaking male rushes to her and releases his sperm. Meanwhile the rightful mate, who himself might be in the act of spawning, is caught unawares. He usually gathers his wits and chases the intruder away, but often the damage is already done. Some of the sneaker's sperm has mingled with the female's eggs, resulting in at least some illicit fertilisations. Such a scenario is often played out in sticklebacks, sunfishes, and various cichlids (see Satellites, below).

In a great number of species (salmon, sticklebacks, sunfishes, minnows, darters, cichlids, wrasses, parrotfishes, gobies, among others) cuckolding part-time while holding a territory full-time does not suit some males. They prefer instead to forego territoriality altogether and to specialise in cheating. Their tactic is the same: they hide near the periphery of a spawning territory, watch what is going on there, sneak in at the critical moment, and try to release sperm as close to a spawning female as possible. This behaviour has been documented and studied for more than 30 years now. The parasitic males have variously been called sneakers, streakers, cuckolders, hiders, furtive males, accessory males, type II males, or interference-spawning males. Because they are small and superficially resemble females[2] (all the better to fool territorial owners), they have also been dubbed pseudofemales, female mimics, and even transvestite males. They may swim around with authentic females, or hide near the nest or territory of the so-called "bourgeois" males, waiting for their chance to steal fertilisations.

Sneakers are parasites. They let bourgeois males do the hard work of defending a territory, building a nest, and developing body ornaments to attract females. Then, seemingly at little cost to themselves, they reap the benefit of at least some fertilisations. If the territory owner provides parental care, the sneaker's progeny will benefit from that too, for bourgeois males cannot tell which eggs were fertilised by them and which were not, and they take care of all eggs indiscriminately.[3]

But there are costs to being a parasitic spawner. Sneakers are pariahs of the high reproductive society. They are despised both by gravid females and by territory owners. In other words, females do not choose them as mates because they are usually too small, and males often recognise them for what they are, despite their disguise, and mercilessly attack them at every opportunity.[4] In salmon, sneakers may even get killed by big males.[5] This makes for a rather stressful existence for the little guys. Indeed, one study on the Mediterranean wrasse *Symphodus ocellatus* has established that sneakers lose just as much weight throughout a reproductive season as territorial males do.[6]

Sperm competition and sperm economy

Sneakers make a special investment in their unconventional way of life. They develop huge gonads. The testes of sneakers can be up to seven times the size of the norm for the species. This is because sneakers practice sperm competition. Their behavioural involvement on the spawning scene is obviously very short; they are in and out. They can only let their sperm do the talking. But the more sperm they release, the greater their chance of grabbing a good share of fertilisations. So, to produce more sperm, sneaker males invest into the development of big testes.[7] (In group spawners – fishes, like herring and cod, that gather in groups and shed eggs and sperm simultaneously and indiscriminately – males also invest in large gonads, which makes sense because in a group spawning sperm from one male are engaged in a race with sperm from many other males.) [8]

Bourgeois males, in contrast, save their strength for territory defence and invest less energy into sperm production. In fact, some of them can be downright stingy with their sperm. The first thing to know here is that male fishes seem to be able to control the number of sperm (the size of the ejaculate) they release during a spawning event. The second thing is that they appear to exert this control in a way that makes sense depending on the circumstances. In some coral reef species for example, a male may need to spawn with many females, sometimes in the same day, and it has been found that males do not apportion sperm equally between all females. With larger females, which usually produce more eggs, males release more sperm. With smaller females, males are less generous.[9] The males do not deign to release more sperm than is necessary for a reasonable fertilisation rate, keeping the rest in reserve for future spawnings. Biologists call this "sperm economy".

Another example of sperm economy can be found in species where males defend a territory that encompasses the domain of many females. These females become the male's harem. It has been found that the larger the harem of a male is, the fewer sperm he releases when spawning with any single female. He wants to make sure that he has enough sperm to go around the full harem, and this means smaller individual contributions when the females are more numerous.[10] (If readers are wondering how researchers manage to obtain information on ejaculate size in field studies, they should prepare to be surprised at how simple it is. Snorkellers hover over likely spawning sites and make sure they do not disturb spawning pairs. But as soon as the deed is done, the snorkellers descend, scatter the fish, and trap all of the milt and eggs – still visible as a white plume in water and still fairly localised – within a large plastic bag. This water is brought back to a boat, mixed, and sampled. The eggs and sperm are stained and counted under a microscope. The tally is multiplied by the dilution factor of the sampling to obtain a final count.)

Males can also adjust the volume of their ejaculate depending on the perceived risk of competition from other males. For example, when mating with a female a male mosquitofish *Gambusia holbrooki* will invest a greater proportion of the sperm reserve in his testes if he has previously been kept in the presence of another male (a potential competitor) as compared to being housed with females only.[11] Male three-spined sticklebacks will also invest more sperm during mating if a TV next to their aquarium displays the image of another male courting as opposed to another male fanning his eggs (parental stickleback males as a rule do not try to steal fertilizations and therefore represent a lower risk of sperm competition).[12] Male bitterlings, *Rhodeus sericeus*, release more sperm into the mussels where females have laid their eggs if there are other males around, at least up to a certain extent.[13] But the response to competition is not always sperm warfare: in some species, overt aggression and more attentive mate guarding is a behavioural alternative.[14]

Success of sneakers

Back to our sneakers: they may dominate in the arena of sperm competition, but they need this nominal advantage because bourgeois males start the game with a big ace up their sleeves. Bourgeois males are *with* the spawning female, next to her right from the start. They can better judge the exact moment when she will release her eggs. They can manage to be as close to the female as possible at that moment. They can synchronise the release of their sperm with the actions of the female. In terms of temporal synchrony and spatial proximity, bourgeois males outperform sneakers.

So what is the end result? Who wins the majority of fertilisations? Researchers can answer this question by capturing all of the actors (males, female, fertilised eggs) on the scene of a spawning event and conduct paternity analyses. Results vary from event to event and from species to species, but as a whole it seems that sneakers almost never fertilise more than half of all the eggs. In fact, they usually do no better than a 33% fertilising rate. And of course, their success is nil when they happen to be away from their station – fed up with being chased all the time.

However, these numbers are still high enough on average to make sneaking a viable tactic. In some populations of sunfishes, parasitic males may even outnumber territory owners. In a few species such as salmon and sunfishes, sneaking appears to be an innate habit, ingrained at birth and fixed for life for the individuals concerned, in the same way that territoriality is the only option for the other males. In the majority of species however, the reproductive role of males is conditional. Depending on the circumstances, the same male may either try his luck as a sneaker or invest into the maintenance of a spawning territory. The incentive to become a sneaker seems to be greater when the male is small relative to the rest of the population, when he is less experienced, and when there are many territorial competitors. (Rather than describing sneakers as behavioural parasites, it might be more charitable to view them as poor sods who are trying to make the best of a bad job; they gamely try to play the poor hand they have been dealt). In a few species, males have been known to switch back and forth between the two tactics, depending on the conditions that prevail at the moment.[15]

Satellites

In a few species, there is an intermediate tactic between sneaking and holding a spawning territory. It consists of defending a small territory, or at least a particular station, at the edge of a big male’s domain. Practitioners of this middle-ground philosophy are called satellites. They are more or less tolerated by the big males. They may breed with small females. They may also steal fertilisations, like sneakers, from the large males. On the other hand satellites can also attack intruders, including other sneakers. Therefore they occupy a buffer zone and form a first line of defence around the big males’ territories.

One of the best examples of satellites is in pupfishes, particularly the Pecos pupfish *Cyprinodon pecosensis*, where males can either be territorial bourgeois, brightly-coloured satellites, or drab sneakers.[16] There are other instances in the cichlid, wrasse, and sunfish families.[17]

Forced copulations

Sneakers circumvent a female's mate choice by surreptitiously partaking in the chosen mate's spawning. Another tactic, rare but nevertheless readily observed in some species, is to somehow mate with a female privately but against her will.

In livebearers, fertilisation is internal. The male deposits his sperm inside the female by inserting his modified anal fin (the gonopodium) into the female's genital pore. Normally, insemination is preceded by a display on the part of the male and acceptance by the female. But some males also try sometimes to approach a female from behind and thrust their gonopodium at her genital pore without prior display. Females normally[18] try to evade such a sneaky manoeuvre,[19] but they don't always succeed. On average however, the success enjoyed by thrusting males is low because of the female's lack of co-operation and the fact that the few sperm injected are often displaced later on by full copulations from displaying males. Yet, for some out-of-favour males this low success is better than nothing.

In livebearers such as sailfin mollies, the swordtail *Xiphophorus nigrensis*, the Gila topminnow, and the mosquitofish, females shun small males when they choose a sexual partner. Small males compensate for this by resorting to thrusting. Careful observations of the social life of these species have revealed that big males display in front of females more often than they thrust, while small males attempt to thrust more often than display.[20]

In another livebearer, the guppy, there seems to be no relationship between body size and thrusting frequency. Instead, thrusting becomes more prevalent when there is a risk that predators could spot displaying males or when there are more competing males in the environment.[21] Moreover, under certain conditions (low light), thrusting predominates in those males that possess longer gonopodiums (be it absolute length or length relative to body size).[22] This suggests that more sperm may be delivered when a longer gonopodium is used in thrusting, and that the propensity for sneaky fertilisations may be co-evolving with gonopodium length. This hypothesis awaits further testing.

Here is another example of forced copulation, this time in a species with the more normal pattern of external fertilisation. In the bluehead wrasse *Thalassoma bifasciatum*, females prefer to mate with big males on traditional spawning sites, but to get to these sites the females must run a gauntlet of smaller non-territorial males. These males intercept the females, relentlessly pursue them, and repeatedly touch them. Sometimes this induces the females to release their eggs – against their true intent, we must presume. All of the small males present on the scene then shed their sperm in what can only be considered a group spawning. As in species where group spawning is the norm, small bluehead wrasse males have bigger testes and release more sperm while spawning than their larger territorial counterparts.[23]

Threesomes

In a few fishes, gravid females are often attended to by two or three males simultaneously. These various males do not appear to differ in status, and they more or less tolerate each other. When the female spawns, the males release their sperm together. This pattern has been observed in some minnows, salmon, and pike.[24]

In many species of suckers (family Catostomidae), spawning often occurs in trios.[25] Two males adjoin a female on either side and seem to press against her. All three fish release their eggs and sperm at the same time. It has been suggested that the pressure exerted in concert by the two males squeezes more eggs out of the female than would normally be released, but this hypothesis has not been tested yet.

Sex changes

Here is a shocking idea: if you are a fish of one sex and your reproductive success is poor, why not try your luck as a member of the other sex?

A diverse array of fishes, mainly marine species, can change sex.[26] Observations of individually marked fish in tanks or in nature have clearly showed that some individuals start their adult life as males, and switch later to females. Or they begin as females, and then become males. This is indicated not only by a change of behaviour, but also by a transformation of the gonads as revealed by biopsies and dissection. Testes are progressively invaded by ovarian tissue. Or ovaries can develop a vas deferens and turn into testes. Among large animals, such capacity for sex change is almost a unique feature of fishes. Mammals, birds, reptile, and amphibians (with the exception of the reed frog *Hyperolius viridiflavus* [27]) are incapable of changing sex in nature.

Sex changes usually happen in species for which the transformation is not too taxing anatomically. Usually these fishes have no elaborate external genitalia, only a duct that leads to gonads. It is hard enough metamorphosing one kind of gonad into another – changing sex can take days, sometimes even weeks – without having also to develop gonopodiums and other accoutrements of the sort.

Another characteristic of sex changers is that for them the influence of age, and therefore of body size, on reproductive success is not the same for both sexes. Small individuals do much better if they are of one sex while large individuals make more babies if they are of the other sex. This latter point requires an illustration.

Anemonefishes often live as male-female pairs within anemones. Because anemones are often widely scattered, it would be difficult for a male to find and spawn with many females during a single reproductive season. Likewise, a female would have a hard time courting many males. So male and female are usually stuck with each other within their little world. Now, because sperm is relatively cheap to manufacture, a small male can fertilise all of the eggs that even the biggest female could possibly produce. In spite of his diminutive size, a small male can also easily defend those eggs because of the protection afforded by the anemone. Therefore, no reproductive advantage can accrue to being bigger for a male. On the other hand, the bigger a female is, the more eggs she can churn out. Therefore it would be advantageous for both members of an anemonefish pair to have the smallest individual be a male and the biggest one be a female. This has resulted in an evolutionary pressure on males to turn into females as they grow bigger. And this is what happens in most anemonefish species: males can change sex and become females.

Elegant work by Hans Fricke has shown that it is not size per se which determines when a male anemonefish changes sex. It is the *relative* size of the two partners and the presence or absence of interactions between these partners. When a male two-banded anemonefish, *Amphiprion bicinctus*, was experimentally forced to live alone in an anemone, he usually did not change sex, or did so very slowly. However, as soon as this lone male was joined by a smaller male, he rapidly turned into a female, reaching the capacity to lay eggs within as little as 26 days. By contrast, if the lone male was joined by a larger male, it was this larger male who changed sex. Absence of a bigger female *and* presence of smaller male combine to trigger sex change in this species.[28]

Something similar can be seen in the nosestripe anemonefish *Amphiprion akallopisos*, where several small males may live together with one female in a particularly vast anemone. Among the males, only the largest one gets to breed with the female. All the others are “psychologically castrated” by the aggressive actions of the breeding male. If the female is experimentally removed, this large breeding male, and only he, immediately starts to turn into a female. Once this is accomplished, the next largest male in line is promoted to breeding status.[29]

Sex change is anemonefishes is only from male to female, not the other way around. If the male of a pair disappears, the remaining female must patiently await the chance arrival of another male, or she must set off on a quest for a new partner (this latter alternative is dangerous, because anemonefishes are poor swimmers and away from the protection of their anemone they are easily captured by predators). Lone females never metamorphose into males. Even when two females are experimentally forced to cohabit within an anemone, the smaller of the two does not turn into a male, even though she suffers constant harassment at the hands of her dominant roommate.

Socially-controlled sex change also exists in the Clark's anemonefish *Amphiprion clarkii*. However, sex change in this species can sometimes be short-circuited by timely migrations. This occurs in dense populations where anemones are clustered together so that movement between anemones takes little time and entails little risk. If the female of a pair disappears, the male will often eschew sex change and go look for another available female nearby. This can work to his advantage because sex changing takes several weeks, whereas finding a new mate in a dense population can be a matter of days only.[30]

Despite its common presence in anemonefishes, male-to-female sex change is rare for fishes in general. More prevalent is the pattern of female-to-male change. This one is in fact fairly common in wrasses, parrotfishes, porgies, damselfishes, seabasses, and gobies. In those species, large males enjoy great reproductive success because they exert exclusive control over extensive harems of females, or they preside over popular spawning territories. This leaves a sizeable portion of the male population with little mating opportunity. Rather than content themselves with the marginal success afforded by sneaking, such small fish may prefer to start out their lives as females, because theoretically all females have access to reproductive males and therefore a guaranteed shot at producing many descendants. Only when they reach impressive physical stature and become more competitive do the most dominant females turn into males, assuming that an opportunity presents itself (i.e., after the loss of a resident male or the sudden influx of many additional females).[31]

As with the male-to-female sex change of anemonefishes, female-to-male change seems to be triggered mostly by social factors. For example, in the cleaner wrasse *Labroides dimidiatus*, which lives in groups that normally comprise a single male and a large harem of females, removal of the male results in the most dominant female changing sex, unless a larger male from outside barges in and takes control of the group.[32] Amazingly, if a larger dominant male appears *after* the largest female has already turned into a male, that female-turned-male can change back into being a female.[33] (Such cases of sex change reversals, also called bi-directional sex changes, are exceedingly rare; to my knowledge, the only other example is the coral-dwelling goby *Gobiodon histrio* from the Great barrier Reef: when two females-turned-males are placed together on a reef, one of the two males can turn back into a female, allowing mating between the two.[34])

In Hawaii, Robert Ross, George Losey, and Milton Diamond conducted the following experiments with the saddle wrasse *Thalassoma duperrey*. They placed a number of lone females in individual pens; all of those fish stubbornly remained female. However, if one of those lone females was joined by a smaller female (or, interestingly, by a smaller male), then she changed sex and turned into a male. If she was joined by a larger female, or by both a larger and a smaller female, she did not change sex; the joining large female did. These results were obtained even when the newcomers were separated from the original occupant by a transparent partition that allowed visual contact but no tactile exchange. The effects, however, could not be obtained when the partition allowed water flow (chemical exchange) but not visual contact. The researchers concluded that through visual cues only, presence of a smaller conspecific *and* absence of a large one can trigger sex changes from female to male in this species.[35]

Sex determination

It is worth mentioning here that in many fishes, sex is not determined at conception or at birth – there are no sex chromosomes.[36] In such species (for example, silversides, Apistogramma cichlids, some livebearers), all individuals come into this world with undifferentiated gonads, or with gonads that look more like ovaries. Only later in life do the gonads become true ovaries or take a left turn and become testes. Environmental factors may affect the direction in which this development proceeds. In the Atlantic silverside *Menidia menidia* for example, low temperatures produce more females while high temperatures favour the formation of males (as is also the case, by the way, in alligators and many lizards).[37] Essentially this means that more females are produced early in the spring, when temperatures tend to be colder, and more males are born later in the summer. Thus females benefit from a longer growing season which allows them to make more eggs. Males manage to manufacture the (cheaper) sperm they need even though their growing season is shorter.[38]

In zebrafish *Danio rerio*, very low oxygen concentration (0.8 mg/L) affects the synthesis of sex hormones and results in slightly more males being produced (about 74 %, as compared to 62 % in normal populations). The extra males are genetically female but have testes instead of ovaries. More work is needed to find out whether the hypoxic conditions that prevail in the hypoxic, so-called "dead zones" of the world's oceans masculinize the fish populations that manage to live there.[39]

In some cichlids and swordtails, extreme pH can nudge gonad development along specific pathways, a very low pH yielding more males. In some cichlids of the genus *Apistogramma*, both temperature and pH can determine sex ratio, with a critical period of exposure 30-40 days after birth. [40]

There is even some evidence, at least in Midas cichlids, *Amphilophus citrinellus*, that relative size and social interactions can determine sex. In the company of smaller conspecifics, Midas cichlid 6-12 months old tend to become males, while other individuals of the same age placed with *larger* tankmates become females.[41]

In eels of the genus *Anguilla*, which includes the American eel *Anguilla rostrata*, more males issue from populations that are crowded. Low population density results in the predominance of females.[42]

In juveniles of the rippled coralgoby *Gobiodon erythrospilus (= rivulatus)*, which can be found on Australia's Great Barrier Reef, gonads do not mature until the fish has met a potential sexual partner. Such a meeting is not a common event, because all the real estate on the corals tends to be already occupied by breeding pairs, and because extensive cruising is discouraged by the presence of many predators (coral gobies are small and make good snacks). The amazing thing is that the encounter with an available adult (most likely one whose mate has just died) will trigger sexual maturation by the arriving juvenile into whichever gender complements the new partner: male if the juvenile has found a female, female if the new partner is male. When it comes to pairing up, anygoby will do, thanks to flexible socially-influenced sex determination.[43]

Sexual maturation

Sexual maturation (gonads becoming capable of producing sperm or eggs; puberty, so to speak) usually occurs once a certain body size is attained. But in some case, social conditions can force a delay. The coralgoby above provided an example: sexual maturation had to wait until a partner was found. There are other examples of social control, and they almost all concern delays caused by the presence of adults.[44] In several species of poeciliids,[45] cichlids,[46] and labrids,[47] as well as in the characin *Corynopoma riisei*,[48] juveniles raised with adults are inhibited from maturing as compared to juveniles raised alone. Usually this phenomenon takes place in males, though in the wrasse *Pseudolabrus celidotus* it is the female whose maturation is inhibited.[49] Maturation is not delayed forever however: eventually the juveniles reach such a large size that they do become sexually mature. But the juveniles raised alone mature earlier, at a smaller size.

Social inhibition of maturation can be achieved either through chemical cues emanating from adults,[50] or by the mere sight of sexually active males,[51] or direct aggression by the more dominant adults.[52]

Social inhibition may be seen as manipulation by the adults to decrease competition for matings, but perhaps the response is adaptive for the juveniles as well. If there are lots of adults to compete with, it may pay to delay maturation and invest energy into more growth so that, when maturation does take place, the emergent adult will be sufficiently large to secure a fair share of matings.

Hermaphroditism

Hermaphrodites play on two fronts: they can produce both eggs and sperm at the same time.[53] (Biologists call this pattern “simultaneous hermaphroditism”. The expression “sequential hermaphroditism” also exists; it refers to sex changers.) No vertebrates beside a few fishes are known to be simultaneous hermaphrodites. The best-studied fish group is a subfamily of sea basses (the hamlets, Serraninae). In these fishes, testes and ovaries are both present within the body but they are separate and they connect to the outside via different ducts. This arrangement precludes internal self-fertilisation. Individuals in fact mate together as pairs, one member playing the role of the female and releasing a few eggs while the other plays the male part and sheds a few sperm. The roles are reversed a few moments later, and this quick alternation between male and female roles continues throughout the spawning episode.[54] This behaviour is called “egg trading”.[55] It may have evolved to prevent individuals from cheating and specialising into the production of sperm only, which is cheaper to manufacture. Such a cheat could not have a high reproductive success because spawning between he and the hermaphrodites would quickly break down once the hermaphrodites realised he could not produce eggs and participate in the egg trading ritual.

The barred serrano *Serranus fasciatus* presents a mating system that incorporates several of the elements covered so far. In this species, all fish start life as hermaphrodites, but in most groups the largest individual loses female function and becomes exclusively male (a sex change of sorts). This male maintains and defends a spawning territory around which the other fish in the group (all of them hermaphrodites) gravitate. As females these hermaphrodites mate only with the big male. As males the hermaphrodites try to sneak and steal fertilisations from the big male.[56]

Few hermaphrodites can self-fertilize. The only well known case is the mangrove rivulus *Rivulus marmoratus*, a tough coastal dweller that can withstand heavy pollution, low oxygen levels, brackish water, and even the lack of water (see “air breathing” in the page on Oxygen). It colonizes small streams that are prone to drying up. Pure females don’t exist in this species. About 95% of a population is born hermaphroditic, the rest being male only. At 3-4 years of age, about 60% of the self-fertilizing hermaphrodites lose their female function and become strictly male. This transformation takes place only if the water temperature is below 20 ºC. Above 25 ºC, all fish remain hermaphrodites. Self-fertilization by the hermaphrodites may ensure reproduction in environments that are harsh and where other members of the species are rare. On the downside however, as opposed to ordinary sex, self-fertilization does not generate much genetic diversity. The presence of males in some populations of otherwise self-fertilizing hermaphrodites suggests a selective pressure to maintain a minimum of genetic diversity.

Parthenogenesis (males, who needs them?)

Some species of fish are parthenogenetic. They are all females. They reproduce asexually. However, some parthenogenetic females still need males, in a roundabout way, from closely-related species. Eggs from these females develop only after being activated through contact with a male’s sperm. However, although the male’s sperm initiates the development of the eggs, it contributes no genetic material.[57] The activated eggs invariably develop into new females. This particular brand of parthenogenesis is called gynogenesis. The best known example is the aptly named Amazon molly *Poecilia formosa*, with the closely related sailfin molly *P. latipinna* and shortfin molly *P. mexicana* acting as trigger males.

It may be asked why male sailfin and shortfin mollies bother to shed sperm over eggs that will not take in their genes. The answer may lie in a study that has showed how female sailfins prefer males they have seen consorting with other females, even when those females are Amazons (in many species, including mollies, females prefer to mate with males they have seen in the company of other females, a phenomenon called "mate choice copying"). The advantage to males of mating with Amazon mollies is that it makes them look good in the eyes of females of their own species.[58] However, there are limits to what these males are willing to do for Amazons: when housed with Amazon females, male sailfins produce less sperm than in the presence of females of their own species. They are less primed (to use the technical term), a physiological analog to sperm economy.[59]

Some female sharks have been known to give birth in captivity after being separated from males for extended periods of time. However, because female sharks can store sperm for a long time after being inseminated by males, there was always a nagging suspicion that the new mothers had mated with a male before capture and simply delayed giving birth. But these doubts have been put to rest, at least in one case. In December 2001, at the Henry Doorly Zoo in Nebraska, one of three female bonnethead sharks (*Sphyrna tiburo*) captured while they were juveniles and kept together for three years without any contact with a male gave birth to one young. Genetic analysis has since proven that no paternal DNA was present in the young, thus confirming parthenogenesis in this shark species.[60] Another shark species, the blacktip *Carcharhinus limbatus*, has recently been confirmed as capable of parthenogenesis also.[61]

Parthenogenesis has been reported in yet another shark species, and with a twist. In captivity, a female whitespotted bambooshark (*Chiloscyllium plagiosum*) has given virgin birth, and one of the female offspring herself gave birth without any contact with a male. This shark has thus provided the first record of second generation facultative parthenogenesis in a vertebrate species.[62]

Parthenogenesis has also been documented in a wild population of smalltooth sawfish (*Pristis pectinate*), an endangered species.[63] It is possible that females resort to parthenogenesis when population density is low and they have trouble finding males for normal sexual reproduction.

Homosexual behaviour

In guppies, a species that practice internal fertilization, males spend a lot of time engaged in sexual behaviour directed at female guppies. As already mentioned, they either perform the sigmoid display (curving their body in the shape of an S), which is an invitation to copulate, or they attempt sneak copulations (trying to suddenly thrust their gonopodium into the genital pore of an unwilling partner). These two behaviours are easy to recognize. Sometimes, it is possible to witness a male directing a sigmoid display or a sneak attempt at other males. A study by Kristin Field and Thomas Waite at Ohio State University in Columbus suggests that the absence of females in the social environment of a male early in his life can cause homosexual behaviour. Field and Waite raised male guppies for 15 weeks in all-male groups or in mixed-sex groups, starting right after sexual maturation in the fish. At the end of those 15 weeks, each male was placed in the presence of three other males and three females. Males raised in the mixed-sex group directed almost all of their displays and sneaky copulation attempts at the females. In contrast, males raised in the all-male groups directed three times as many sigmoid displays to the other males than to females, and almost all of their sneaky copulation attempts at the other males, even though females were present. The scientists went on to warn that conservation breeding programs (not necessarily in guppies but in other fish species) should be careful about housing fish in single-sex groups.[64]

Many cichlid fishes form mating pairs. A male and a female develop a bond and start preparing a nest site together and defending a territory around it. Eventually the female lays her eggs, the male fertilizes them, and both protect the eggs. In cichlids such as the orange chromide and the jewel fish, if only females are housed together, two individual females may pair up. One or both of them may lay eggs, which of course remain unfertilized. Such homosexual behaviour does not happen if mature males are also present in the environment. (In contrast, male homosexual pairs never form, even in all-male groups. Male cichlids are just too aggressive towards each other. Even in females, aggression puts up a formidable barrier to homosexual pairing.)[65]

Wikipedia lists at least 15 species of fish in which evidence of homosexual behaviour exists. Even within these species however, homosexuality does not appear to be notable under natural conditions. See:

http://en.wikipedia.org/wiki/List_of_animals_displaying_homosexual_behavior

Conclusion

Fishes are said to be “lower” vertebrates. Technically this expression only means that fishes developed in the course of evolution earlier than amphibians, reptiles, birds and mammals. Yet the adjective “lower” cannot help but to convey an impression of inferiority. This is unfortunate, because the notion of what is inferior and what is superior depends on the point of view. For example, as compared to birds and mammals, fishes have retained an amazing plasticity in the development of their sexual anatomy and sexual behaviour. This has opened to them several alternatives to the “traditional” sex roles of big competitive males and smaller choosy females. These alternatives – sneaky males who look like females, males who can control their output of sperm, sex changers, hermaphrodites – are not inferior. The proof of it is that after so much time since fishes first appeared on earth, these seemingly odd reproductive tactics are still around, enabling their adherents to contribute specific genes to the next generation.

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[1] For references and a thorough review on this topic, see: Taborsky, M., 1994, Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction, Pp. 1-100 *In* Advances in the Study of Behavior, Vol. 23 (Slater, P.J.B., Rosenblatt, J.S., Snowdon, C.T., and Milinski, M., eds.), Academic Press, San Diego.

[2] Female mimicry can go beyond body size and colour. The plainfin midshipman is a very vocal fish. Big males attract females to their nest by broadcasting long-duration hums. Their sonic muscles are powerful. In contrast, small males try to hide within the nest of the big males and steal fertilisations. They are small like females and also mimic the short-duration grunts of females. Their sonic muscles are poorly developed. In this species, female mimicry by sneakers extends to vocal behaviour. See: Brantley, R.K., and Bass, A.H., 1994, Alternative male spawning tactics and acoustic signals in the plainfin midshipman fish *Porichthys notatus* Girard (Teleostei, Batrachoididae), Ethology 96, 213-232; Goodson, J.L., and Bass, A.H., 2000, Forebrain peptides modulate sexually polymorphic vocal circuitry, Nature 403, 769-772.

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[4] Females often interrupt their nest inspection or their spawning activities with bourgeois males when they see sneakers approaching. Thus, bourgeois males who succeed in keeping their territorial boundaries free of sneakers benefit: not only are they able to monopolise all fertilisations with a given female, but more females accept to spawn in their nest. In the wrasse *Symphodus ocellatus*, experimental removal of sneakers around some nests led to a 5-fold increase in the spawning rate enjoyed by the bourgeois males at those nests; see: van den Berghe, E.P., Wernerus, F., and Warner, R.R., 1989, Female choice and the mating cost of peripheral males, Animal Behaviour 38, 875-884. Also: Alonzo, S.H., and Warner, R.R., 1999, A trade-off generated by sexual conflict: Mediterranean wrasse males refuse present mates to increase future success, Behavioral Ecology 10, 105-111; Alonzo, S.H., and Warner, R.R., 2000, Dynamic games and field experiments examining intra- and intersexual conflict: explaining counterintuitive mating behavior in a Mediterranean wrasse, *Symphodus ocellatus*, Behavioral Ecology 11, 56-70.

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