HUMANE SOCIETY INTERNATIONAL

About Fish

Background

Fishes can be categorized into one of two groups according to their skeleton-type: cartilaginous fishes (Superclass Chondrichthyes[1]) or bony fishes (Superclass Osteichthyes[2]). Sharks, rays, sawfishes, and ratfishes are common examples of cartilaginous fishes with characteristics like replaceable teeth, stiff fins, and scales called "dermal denticles" which have the same structure as the human teeth. Cartilaginous fishes grow new scales when needed, as the individual scales do not grow continuously with the fish. There are over 1,000 separate species of cartilaginous fishes, 470 of which are skates, rays, and sawfishes, while 450 are sharks. As their skeleton is made of cartilage instead of bone, fossil evidence and evolutionary knowledge of sharks comes primarily from fossilized teeth. The oldest fossils found of cartilaginous fishes, however, are from scales thought to be 455 million years old, from the late Ordovician. The oldest tooth dates back to 409 million years ago, or the early Devonian period.[3] Many of the currently known shark families have existed, largely unchanged, for approximately 100 million years.[4]

Bony fishes, or teleosts, are thought to have evolved during the Mesozoic era (70-155 million years ago) alongside birds and mammals.[5] In contrast to cartilaginous fishes, bony fishes typically have non-replaceable teeth (if teeth are present), flexible fins, and scales that grow throughout the life of the fish.[6] Today, they are the most plentiful and varied among all vertebrates with more than 24,000 documented species.[7] Bony fishes are known to inhabit great depths, a great variety of habitats, and waters as cold as -2° C (28 °F), or as warm as 42° C (108 °F).[8] The average lifespan of fishes varies from approximately 1-120 years.[9]

Fishes are found in almost all aquatic environments: hot springs, the Antarctic, high elevation lakes (up to 17,000 feet), 23,000 feet under the sea, near deep-sea thermal vents, and in salty and fresh water. Some species have even developed air-breathing organs, which allow them to live and breathe out of water.[10] While most fishes live only in one type of environment (e.g. freshwater or saltwater), those that migrate between the two habitats have developed bodily processes that allow them to quickly adjust to changes in salinity.[11] The majority of fishes in the ocean are littoral (in that they live near the shore). Of those oceanic fishes living in well-lit shallower portions of the ocean, most are large predators or fishes that feed on small plankton. The fishes that live further out in the ocean typically occur at great depths. While most oceanic fishes live in the tropics, those located elsewhere are typically found in only one of the hemispheres (northern or southern).[12]

Fishes have a number of unique adaptations that allow them to function in their environments. Senses like vision, hearing, and smell are present in most fishes, while some species can detect water movement,[13] create and interpret electrical impulses,[14] and navigate using the sun.[15] In fact, sharks and skates are sensitive to differences in voltage of 0.01 microvolt (or one ten-billionth of a volt) per centimeter. This level of electrical detection is believed to be the greatest in the animal kingdom.[16]

Some fishes are well-known for their long and strenuous migrations; many more species frequently travel shorter distances between three habitats types: reproductive (spawning), feeding, and refuge.[17] The feeding and refuge habitats may be geographically close, but the main spawning and feeding grounds are usually distinct and separate.[18] Displacement due to floods, drought, or daytime exploratory activity are other causes of migratory movements.[19]

Researchers have been largely unable to determine whether fish sleep, but anecdotal accounts of night sluggishness in pet fish as well as divers' observations of fish "settling down for the night" by moving into crevices, coral heads, or other areas of cover suggest that some degree of rest may be taking place.[20]

Fishes occupy a wide variety of habitats, eat foods ranging from zooplankton to large fish and mammals. They exhibit an array of behaviors in social contexts and reproductive settings that are closely related to, or in some cases distinct from, those seen in mammals. Their shoaling, or schooling, behaviors mimic those seen in terrestrial herding animals. Some fishes are territorial, while others use different techniques to forage and avoid predators. Various species possess large home ranges, while others occupy very small home areas.[21] A number of species exist within dominance hierarchies, where the dominant fish is often larger than subordinates. However, disagreement remains over whether the large size is a cause or effect of the fish's dominance.[22,23]

Several fishes have evolved hermaphroditism to boost their reproductive success in contexts where the ratio of males and females frequently shifts.[24] Both monogamous and polygamous mating systems are observed in fishes.[25] Less than one percent of all fish species are semelparous, in that they die after spawning; most fishes are iteroparous, reproducing over several seasons, even when significant migrations are involved.[26] Although most fishes are ectotherms (cold-blooded), several species like the short-fin mako shark, and some mackerels and tunas exhibit endothermic, or warm-blooded, tendencies in some parts of their body.[27] Visual feeders are understood to be largely diurnal, or active during the day, but new evidence suggests that even these species show nocturnal tendencies at certain times.[28]

Fishes use a wide variety of methods to avoid being detected by predators. Some species resemble non-edible items like the "leaf fish," while others have evolved shading, mirror-like body surfaces, or transparency to confuse predators.[29] Spines, bony armor, venomous glands, and electric organs are also physical characteristics used by some species for protection.[30] Other tactics used by fishes to avoid being eaten include: fleeing, refuging, gauging, mobbing, shoaling (schooling), diversion (tail eyespots), alarm signals, and feigning death. Refuging, when fishes hide in debris, crevices, or substrata can take interesting forms such as fishes who associate themselves with potentially dangerous organisms like the remora and shark, and fishes like the clownfish that take shelter in anemones.[31,32] Individual shoaling fish occasionally "gauges" predators by approaching and quickly lunging at them, potentially to determine the predator's hunger level. Unexpectedly, in a study of cichlids engaging in this behavior, more subsequent attacks were directed at those fish that did not engage in the "gauging" behavior. Both freshwater and marine fishes have been observed inspecting predators in this way, but only schooling fishes engage in this behavior.[33]

Although a great deal of variation exists among fish species as it relates to habitat, diet, and behavior, the following bony fishes will be considered in greater detail: salmon, trout, bass, tilapia, and catfish.

Natural Behavior

Senses

Most species of bony fishes have well-developed eyes whose retinas contain color-sensitive cones. In addition, results from behavioral tests demonstrated their ability to discriminate among colors. Fishes who live in dark, deep waters possess more rod cells that enhance vision in low light, while shallow water fishes possess more cone cells, allowing them to see better in conditions with increased light. Fishes that live in the blue water of reefs and the open ocean have vision most sensitive to shades of blue and green. Research also suggests that fishes gain better visual accuracy with age.[34] Salmon are known to have keen vision even before they reach adulthood,[35] with some species relying solely on vision to find prey.[36] Similarly, trout are believed to depend on vision when foraging,[37] with larger, older fish more able to detect prey at a distance than young trout. They are also believed to distinguish between colors, particularly red, green, and blue. A unique cone cell in the eye of trout and other salmonids suggests that, unlike humans, they can detect ultraviolet light,[38] while trout are thought to be sensitive to polarized light.[39] Since bass and tilapia are known to be active during the day (diurnal), they are also believed to rely heavily on vision in their daily lives. Some species of bass and tilapia, however, also show signs of nocturnal activity.[40] [41] In contrast, catfish do not rely on vision, but use chemical cues and other signals to survive in their environment.[42]

Fish are most sensitive to low frequency sounds below two to three kHz;[43] by comparison, humans are responsive to sounds with frequencies above 15kHz.[44] As sound travels through water, it moves through the fish's body and makes the inner ear's otolith organ vibrate. This vibration triggers movement in the sensory cell hairs embedded in the otolith, which signals the fish's brain. Interestingly, the swim bladder, an apparatus dedicated to flotation and depth modification, is an integral component of a fish's hearing as it transforms pressure waves from the surrounding water into pulsating movements that are received by the ear.[45] Communication through sound seems to be common in fish; aggression, courtship, and warnings can be communicated through low frequency sounds that are often described as grunts, croaks, hums, moans, thumps, pops, buzzes, clicks, howls, knocks, and snores.[46] Fish are believed to be able to determine the direction and distance of a sound source as well as discriminate among calls with different pulse patterns, amplitudes and frequencies.[47] Though researchers have yet to identify the lower limit of sound sensitivity in fish, juvenile chinook salmon and rainbow trout attempted to escape when exposed to artificially generated sounds at 10Hz. Sounds at this level are considered "infrasound" and are too low for humans to detect.[48] Catfish hearing is enhanced due to the weberian apparatus, four to five modified vertebrae that connect their swim bladder and inner ear which carries sounds and pressure change signals to the brain.[49]

Olfaction, or chemosensory information, is thought to be important for fish in finding food and mates, avoiding predators, and navigation.[50] However, olfactory signals may become diluted in water and move slowly without a strong water current.[51] Researchers increasingly attribute migratory abilities in salmonids to an extensive use of chemosensory cues. Salmon and trout are thought to be more skillful at using olfactory information than other kinds of fish.[52] Juvenile Atlantic salmon and rainbow trout have both demonstrated their ability to use chemosensory information in distinguishing between kin and non-kin.[53] Furthermore, one study found that Brown trout were more nocturnally active than previously thought, leading researchers to conclude that chemical cues must inform their night-time foraging activities, unless they had developed excellent vision in low light, a rare phenomenon in salmonids.[54] Since a number of bass species embark on significant migrations,[55] a reliance on chemosensory cues, among others, is likely. Olfaction is an important tool for tilapia; the Mozambique tilapia *(Oreochromis mossambicus)* use olfaction to determine a female's reproductive status, while juvenile Nile tilapia (*Oreochromis niloticus)* use chemical communication to aid in individual recognition and to reduce aggressive interactions.[56] Catfish rely heavily on chemosensory information and are capable of retaining the chemical signals in their memories for extended periods of time.[57]

The lateral line is a series of pores that line the flank of a fish's body from the head to the tail. It was originally thought to be associated with the sense of touch or hearing,[58] but recent evidence suggests it is used for detecting subtle levels of water displacement in the immediate environment. This sensory system is best used over short distances though, as water disturbances tend to dissipate quickly. Not only can the lateral line assist fish in locating potential prey, it also helps them navigate within their surroundings by detecting water movement around nearby objects. However, its capacity to independently direct fish toward a food source can be limited as Fraser and Metcalfe found with Atlantic salmon *(Salmo salar)*. The species is known to rely on sight to locate prey, and when the environment was devoid of light, the salmon were unable to locate prey, even with the help of their lateral line.[59] In contrast, brook trout *(Salvelinus fontinalis)*, who locate hiding places by sight during the day, were able to locate an area of cover in the presence of no other cues except those perceived by their lateral line.[60] Cichlids, the family to which tilapia belong, are known for having an interrupted lateral line that does not continue unbroken from head to tail.[61] Catfish, like most species of fish, use their lateral line to detect prey and understand the landscape of their environment.[62]

Electroreception abilities are found most often in fish species who inhabit murky waters or feed at night. Catfish have the ability to detect electric stimuli from hidden prey as well as distortions in the electric field caused by other fish.[63] One species of catfish is even capable of producing electric discharges up to 600 volts.[64]

Salmonids, like salmon and trout, are thought to use the earth's magnetic field for navigation during their journeys back to their natal home stream for spawning. However, this ability has also been found in non-migratory rainbow trout who were observed orienting themselves according to the earth's magnetic field, but later assumed random positions when exposure to the magnetic field was prevented.[65] Mann and Sparks helped explain this phenomenon by describing the magnetite particle chains present in the front of sockeye salmon *(Oncorhynchus nerka)* skulls, which enable the fish to perceive the intensity and direction of magnetic fields.[66]

Migration

Migrations, as described by Lucas and Baras, are synchronized movements that are larger relative to the average home range for that species and which occur at specific stages of the life cycle.[67] Even though many fishes migrate short distances between spawning, feeding, and refuge habitats, salmon and trout are well-known for their strenuous spawning-driven journeys from the ocean to their natal stream.

A number of factors dictate whether an individual fish engages in migratory behavior: genetics, hunger, homing, predator avoidance, and other environmental conditions like temperature, water flow and quality.[68] Cues like geographic landmarks, celestial information, water currents, electric and magnetic fields, olfaction, salinity, and memory may assist fish as they navigate during their migration.[69] Juvenile Atlantic and Pacific salmon migrate to the ocean where they remain until they return to the stream of their birth as sexually mature adults. Some adults leave the ocean after only one winter while others may stay at sea for two or more years before embarking on their upstream migration.[70] Prior to and during their return migration, they cease to eat, drawing on their fatty energy reserves to survive.[71] [72] Two Pacific salmon, the coho *(Oncorhynchus kisutch)*[73] and sockeye,[74] exhibit a "semelparous" life cycle that is characteristic of several species of salmonid; they breed only once, at the end of their long migration, and die shortly thereafter. In contrast, other salmonids like Atlantic salmon, rainbow trout, and steelhead trout are "iteroparous" because adults breed more than once.[75]

Sea trout and brown trout have been determined recently to be the migratory and non-migratory forms, respectively, of the same species *(Salmo trutta)*. Sea trout, unlike salmon, are believed to eat as they migrate back to their natal river[76] and show a greater degree of iteroparity than many salmon.[77] Although brown trout do not migrate over great distance, some may travel tens of miles to spawn, while others choose more secluded areas of their home stream for reproducing.[78] Previously, the consensus was that stream-dwelling trout led sedentary lives, but researchers increasingly suggest that the difficulty inherent in tracking fish movements may have misled researchers. For instance, Cox discovered that Batten Kill brown trout, a species previously considered sedentary, were in fact dependent on large home ranges and engaged in longer spawning migrations than previously thought.[79].

Bass exhibit a range of migratory patterns. Striped bass are generally considered anadromous, as they live predominantly in the ocean but return to rivers for spawning. However, in the extremes of their geographical range, the Gulf of Mexico and the St. Lawrence River, striped bass are potamodromous, staying in rivers, since coastal waters may be too warm or cold, depending on the location.[80] Other bass populations exhibit more restricted movement, travelling long distances only when negotiating fluctuations in seasonal water temperature.[81]

Cichlids, including tilapia, are believed to engage in minimal migratory behaviors, most likely limited to small seasonal movements in reaction to environmental changes, like flooding. However, researchers contend that more investigation is required before ruling out migratory abilities in cichlids.[82] Lucas and Baras propose that the ecosystem dictates to what extent a species migrates. Lake-dwelling tilapias are more sedentary while individuals who live in the Niger River delta in Mali, for example, are more active, moving into the floodplain following heavy rains and departing before the water disappears.[83]

According to Lucas and Baras, the only species of catfish for which evidence exists of an anadromous migratory pattern is *A. madagascariensis.* Other catfish known to migrate are South American loricariid catfish and several tropical catfish that do not engage in egg guarding.[84] Barthem and Goulding, assert that many large catfish of the Amazon Basin can be considered migratory because of their regular travel from one habitat, or location, to another during the year or at different stages in their life cycle. Most catfish migrations in the Amazon are considered potamodromous, occurring in freshwater only, but three catfish species show a diadromous pattern. Although they do travel over considerable distance toward the ocean, they stop short of the coast upon reaching their estuary destination.[85]

Spawning

Fish utilize a variety of mating systems. Species that require bi-parental care for their young, or who are part of very small populations, are often monogamous, but such pairings are not necessarily long-lasting.[86] Polygamous mating is most common in fish and occurs in several forms: polygyny, polyandry, and promiscuity. Marine fish are often polygynous in that one male mates with several females, while females usually mate with one male. Polyandry, a rare type of mating system seen in some anemone fish, involves one female mating with several males and each male mating with only one female. Promiscuity, a common mating system in nesting fish, involves several partners per individual fish.[87]

According to Wootton's description, hermaphroditism (a phenomenon studied by Warner and Shapiro) occurs in several species of fish. Simultaneous hermaphroditism, when an individual possesses male and female anatomy at the same time, is most common in very small populations in which an individual's likelihood of finding several potential mates is low. Sequential hermaphroditism, however, is more common and causes a fish of one gender to transform into the other gender as a result of a change in the group's gender ratio or the absence of a dominant individual.[88]

In species that require parental care, one or both genders often prefer large mates whose potential to either provide protection for the nest (males) or contribute more eggs (females) is increased.[89] As fish have indeterminate growth,[90] in that they continue to grow with age, large individuals are perceived by potential mates to be healthy, have a proven ability to find food and possess the knowledge necessary to survive.[91] For species in which paternal care is common, the female often chooses larger males[92] based on their likely good health and ability to defend the nest.[93] Additionally, females have shown a preference for males with symmetrical markings and high quality territories when selecting a mate.[94] Species that do not show mate choice are those that rarely encounter the opposite sex and must take advantage of whatever opportunities arise, as well as those that engage in "group spawning" where the eggs and sperm are released simultaneously by all members of a school.[95] Although some species of fish, like sharks and seahorses, are known to engage in internal fertilization,[96] approximately 85% of bony fish families use external fertilization.[97]

Although Pacific salmon are highly semelparous, females occasionally survive to breed again.[98] Atlantic salmon, on the other hand, show more iteroparous tendencies.[99] Spawning typically begins in the fall when females begin searching for areas with silt-free gravel[100] in which to lay their eggs six to twelve inches deep.[101] Adult male coho salmon possess a hooked nose, or kype, for male-male competition during spawning. However, some males known as "jacks" do not develop the kype, but instead remain hidden from fighting males and engage in "sneak" fertilizations with females.[102] Depending on her size, a female may lay from 2,000-15,000 eggs.[103] Female coho salmon typically return to rivers to breed after three years. After the female excavates a nest in the streambed she deposits her eggs. Large males then fight to get access to the nest to fertilize the eggs, but occasionally smaller jacks may sneak in and fertilize the nest instead.[104]

Spawning behavior in trout resembles that of salmon, but trout often prefer finer gravel for spawning as well as different locations.[105] If ideal-spawning sites cannot be located, trout may lay their eggs in less-than-suitable areas, or forego spawning altogether. Mills described Stuart's account of the importance of water temperature for trout nest placement. If the temperature is not suitable, the female will disregard even readily accessible areas. If she does not lay her eggs as a result of a lack of available nest sites, the female's body will reabsorb them. However, firm collections of chorion membranes have been found inside female carcasses, leading some scientists to theorize that these unabsorbed masses are responsible for the deaths of multiple females every year, a consequence of inadequate spawning areas.[106]

Striped bass are iteroparous, spawning several times over their lifetime. Males mature by age two, while females are sexually mature at three to four years old.[107] Adults utilize rivers, fresh waters affected by tides, and estuaries for spawning and nursery areas.[108] Migrations of over a hundred miles are not unusual[109] for bass to reach their shallow, turbid, freshwater spawning grounds.[110] However, unlike salmonids, striped bass have not been proven to migrate back to their natal streams for spawning.[111] Largemouth bass can spawn upon reaching one year of age or at least 10 inches in length. Males construct nests once the water temperature reaches 18-24° C (65-75 °F) in their preferred substrate of sand or gravel. Males prepare the nest site, typically twenty inches in diameter and six inches deep, by fanning the substrate with their fins and bodies.[112] The male will circle the nest in an effort to entice a female and when she arrives they circle the nest together. To spawn, they tilt on their sides so that their vents are in close proximity to each other before releasing their eggs and sperm. Females usually possess 2,000-7,000 eggs per pound of body weight, with an average of 4,000 eggs, but she usually releases only a few hundred eggs per nest.[113]

The age at which tilapia reach sexual maturity depends on a number of factors like habitat and environmental conditions. Fish in large lakes reach sexual maturity later than those raised in small ponds. Compared to other fishes, tilapia reach a spawning age relatively quickly, in three to six months in Mozambique and Nile tilapia, respectively.[114] Reproduction does not occur at temperatures below 68 °F but is most likely at 80 °F and above.[115] Female tilapia do not advertise their mating readiness because they ultimately choose which male to mate with. Males engage in territorial behaviors at designated "leks," where interested females approach them. Upon a female's arrival, males engage in typical mating behaviors like nest digging, trembling, and circling. Once the female chooses her mate and spawns, she carries the fertilized eggs in her mouth and incubates them.[116] Several species of New World cichlids are well known for their monogamous pairings, a rare mating system among fish.[117]

Catfish spawning is challenging to observe since the fish often inhabit murky waters. A variety of spawning techniques have developed in catfish, from open-substrate spawning, to mouth brooding, and even internal fertilization in certain species.[118] [119] The piramutaba, a catfish from the Amazon, is thought to be of breeding age at three years old[120] while the flathead catfish *(Pylodictis olivaris)* may take as long as six years to attain sexual maturity and prefers water temperatures between 75 and 80 °F for spawning.[121] Channel catfish males are monogamous, keeping only one mate per mating season. Females spawn once a year usually between May and July, although the monogamous pairing is established earlier.[122] Potential nest sites are often weedy areas near shore, in tunnels, or under rock ledges; males prepare the nest for spawning by fanning the area with their fins and bodies.[123]

Territoriality

Lucas and Baras define a "home range" as a well-defined region of space to which fish or other animals restrict their activities.[124] While some experts use "home range" and "territory" interchangeably,[125] others characterize territories as specific areas, much smaller than home ranges, that can be defended against intruders.[126] Territorial behavior has been observed in 67% of the fish families that have been well studied.

It has been theorized that in the case of fish, if parental care is more pervasive, territoriality would also be more common.[127] Fish who live in coral reef habitats tend to display more defensive and territorial behaviors. Grant proposed that the high productivity of these reef environments allows individuals to occupy small home ranges, which are more easily protected than larger areas.[128] Godin elaborated that intruder pressure, and resource density and dispersion, dictate whether fish defend territories. Due to their less prolific environment, freshwater fish do not show such defensive strategies as it relates to food, although they will defend a food resource in the laboratory when it is arranged in such a way that it can be protected. Researchers have found that mates, spawning sites, nests, and offspring elicit defensive and territorial behavior more often than food in many fish.[129]

Observers of juvenile salmonids categorize the fish into one of three groups according to their feeding and defensive strategies: territorial, non-territorial, and floater. Territorial individuals establish “stations” where they remain for long periods and from which they capture prey. Floaters, on the other hand, feed while swimming, but must remain on-guard, as they will likely be pursued if another fish’s territory is encroached upon. Non-territorial fish often join schools but rarely engage in aggressive behaviors; they expend considerable energy as they search for food and negotiate the water current.[130] According to Mills, young salmon tend to remain in their natal stream “territories” for considerable periods of time prior to their seaward migration.[131] Braithwaite also observed juvenile Atlantic salmon (parr) living within home ranges while they remained in freshwater.[132] Keeley and Grant found that the territory size of juvenile Atlantic salmon was determined by the inhabitant’s body size: larger fish required larger territories. As a result, they theorized that population density would decrease as fish increase in body size. While they found evidence that territory size decreased as the quantity of food increased, their data did not find as strong a correlation as had previous studies.[133]

While studying the homing behavior of stream-dwelling fish, Halvorsen discovered that the size of a home range varies from 30-300 feet long, depending on the species and stream environment.[134] Young found brown trout from streams in Wyoming to be largely nocturnal with an average home range size of 123 feet. Not only were they found to be more active than previously thought, brown trout in this study traveled distances comparable to three times the size of their home range, in each 24-hour period.[135] Cox uncovered supporting evidence when he discovered that, not only were Batten Kill brown trout embarking on migrations, potentially to natal habitats, they also occupied sizeable home ranges.[136] While studying the foraging behavior of brown trout from a Pennsylvania stream, Bachman observed that the home ranges established by juveniles in their first two years of life changed little with time and were, on average, 166 ft^2 in size. Additionally, no individual fish appeared to have sole use of his or her home range and no territory defense took place.[137] Keeley and McPhail found that juvenile steelhead trout defended territories of similar sizes to those of juvenile Atlantic salmon. They also observed larger juveniles in deeper, faster water than their smaller counterparts. Their findings supported previous theories that territory size decreased as the quantity of available food increased.[138]

While studying the hunting behavior of Florida largemouth bass, Annett discovered the frequency with which bass gathered in hunting groups with other bass, or bluegill. These groups most likely facilitated the location and capture of elusive prey. Annett referenced other researchers’ findings that bass occupy semi-stable home ranges and elaborated that these home ranges likely provide bass with opportunities to encounter other fish and gather into hunting groups.[139] Juvenile sea bass have been observed occupying home ranges, or territories, and sharing them with other individual(s) on occasion.[140] Smallmouth bass were also observed in specific home ranges that they occupied for the majority of the year. In a study of habitat use in smallmouth bass, Todd et al determined that 75% of the fish that left their home range to spawn eventually returned to their home area.[141]

Several cichlid species, including the threespot tilapia *(Oreochromis andersonii),* exhibit home range behavior, staying within an area no more than 600 feet in size. However, the home range size does vary considerably, with the pink happy (another cichlid) claiming a home range approximately 1,200 feet in size.[142] Since cichlids have more developed parental care behaviors than many other fish, they display considerable territoriality and vigilance when guarding their eggs or when trying to attract a mate, as seen in male Mozambique tilapia.[143] [144]

Catfish are largely solitary, often reacting aggressively when their home area is disturbed, as observed in Japanese bagrid catfish *(Pseudobagrus ichikawai).* Adult males are particularly territorial, protecting their shelters and spawning sites in river systems. Their territorial behavior is thought to be exacerbated by the limited number of refuge and breeding sites in their ecosystem.[145] In contrast, captive catfish have shown a considerable ability to adapt to sharing their environment when given no other options.[146]

Foraging

Fish employ a variety of techniques to forage for food; some species use a “sit and wait” strategy while others join schools of fish. Researchers have established that many fish rely on sight to obtain food and navigate within their environment. Moreover, Douglas and Braithwaite uncovered the use of landmarks by foraging goldfish *(Carassius auratus)* and Atlantic salmon, respectively.[147] Not only have both species shown their ability to use other objects to help them locate hidden food, goldfish adapted their search according to the object's size, illustrating their understanding of depth and distance.[148] Juvenile Atlantic salmon, on the other hand, exhibited their ability to distinguish between two similar landmarks to determine the location of hidden food, as well as use alternative cues when the visual signal was no longer reliable.[149]

Researchers agree that salmon and trout are primarily visual feeders.[150,151] However, Brown described an important difference in the foraging habits of Atlantic salmon and rainbow trout. Salmon foraged only for items suspended in the water column, while rainbow trout pursued floating food as well as that which had settled on the substrate.[152] For fish that have established a feeding position or territory, they will likely employ a "sit and wait" strategy whereby they swiftly grab any prey items that pass by with the current.[153] For others, foraging takes place while swimming and artfully dodging other fish's territories.[154] Bachman observed brown trout utilizing the "sit and wait" technique; in fact, 86% of the trout's time was spent waiting for prey to drift by, an energy efficient method compared to actively foraging off the substrate which was observed 15% of the time.[155] Even though salmonids are known to serve a vital role as predators in cold-water streams, little is known about how they choose prey and other facets of their feeding behaviors,[156] other than their opportunistic nature.[157]

Largemouth bass have been observed foraging for schooling fish by selectively pursuing individuals that are "different" - those of a different size or color from the group.[158] Annett discovered the Florida largemouth bass' tendency to forage in groups, a practice that most likely enhances the location and capture of schooling, hiding, or well-guarded prey.[159] Researchers surmised that "drift feeding," as practiced by salmonids, while efficient for juvenile bass, is an unwise use of energy for adults who tend to avoid areas with swift currents.[160] Florida largemouth bass were also observed focusing their hunting on habitats rich with vegetation that attracted their usual prey of sunfish and spotted tilapia.[161]

Since tilapia eat much smaller organisms like plankton, detritus, invertebrates, larvae, fish eggs, fish larvae, and aquatic plants, they are considered filter feeders. The mucous secreted by their gills allows them to take in small food items as they swim.[162] [163]

Catfish rely on sound and olfaction, as opposed to vision, when foraging for their prey[164] that includes insects, algae, fish, crawfish, and snails.[165] The weberian apparatus, unique to catfish and several other species, allows catfish to use their complex anatomy to recognize the sounds of potential prey. The barbells, or whiskers, common to catfish afford them a tactile understanding of their environment. Furthermore, several families of catfish are known to possess olfactory cells on their bodies and barbells, accentuating their ability to function in their turbid environment.[166] Although catfish are widely regarded as primarily bottom-feeders, many Amazonian catfish feed throughout the water column.[167]

Social Behavior

Fishes exhibit a range of social tendencies; some live largely solitary lives while others prefer the protection and company of schools. Familial relationships vary in importance from species that recognize and reduce aggression toward those with whom they are related to those that do not. Communication also plays an important role in communicating social and reproductive status.

Schools provide fish with protection from predators, as each individual's chance of being taken is decreased when part of a group.[168] These schools of fish, or shoals, may be more or less tightly grouped, with loosely knit groups common in low light conditions and tightly grouped schools likely when predators are nearby.[169] The environment often dictates what type of social arrangement the fish adopt. Large bodies of water, like lakes and oceans, more often require fish to accept the added protection of a school, while streams and shallow lakes allow individuals to remain solitary. Schools of fish not only decrease a fish's predation risk but they also increase the likelihood of finding food as many individuals are foraging at once. However, this common desire to forage can result in considerable competition for food. Herring and mackerel are often found in schools, while other larger, territorial, and predatory fish tend to school only as juveniles[170] or on other rare occasions.[171]

As Atlantic salmon and rainbow trout age, aggressive interactions increase, with fin displays and head-down postures replacing the chasing and nipping common in young fish.[172] As juveniles, salmonids are able to recognize kin by chemosensory signals and show fewer aggressive behaviors toward their relatives. In fact, smaller territories are kept by dominants when they are in the presence of family. Interestingly, young rainbow trout show these kin-friendly behaviors even in poor quality habitats, which allows their subordinate kin to gain more weight when compared to non-kin.[173] Similarly, Nile tilapia direct less aggressive behaviors toward fish from their "social group" when compared to their interactions with unfamiliar fish.[174]

A connection between body size and dominance has been observed in many fish species. However, scientists increasingly question whether large body size is not so much the cause of a fish's dominance as the result of superior access to prime feeding areas enjoyed by dominant individuals. Yamamoto described several studies in which large body size, relative to others, proved advantageous to brook, rainbow, and steelhead trout when attempting to establish dominance. While those results supported the traditional view of a connection between body size and dominance, Huntingford discovered that body size was not a good predictor for dominance status in Atlantic salmon.[175] While studying Atlantic salmon, Metcalfe uncovered a significant linkage between the standard metabolic rate (SMR) and body size. He discovered that young fish with high metabolisms exhaust their yolk sac reserves sooner and, as a result, must forage for solid food earlier than fish with slower metabolisms. Fish with higher metabolisms, therefore, grow faster and attain a more dominant status over their smaller counterparts. Interestingly, this high metabolic rate could be disadvantageous during a food shortage, as it requires the fish to expend more energy per activity than those with lower metabolisms.[176] Yamamoto found supportive evidence in masu salmon *(Oncorhynchus masou)*. Their body size did not affect dominance contests, but their metabolic rate was associated with social assertiveness. These more dominant individuals gained access to food more readily and became larger fish as a result, but their increased size was due to their dominance. Social hierarchies are important in cichlids, like tilapia, who establish dominance hierarchies, and whose body size appears to be an important factor in determining an individual's rank. Furthermore, male Mozambique tilapias release urine, mixed with other substances, that communicates his dominance status to potential mates.[177]

Communication appears to be common in fish, particularly via sound, in the contexts of competition, territoriality, aggression, and mating.[178] Olfaction is another widespread form of communication that assists fish with predator avoidance through alarm signals and in attracting mates.[179] For instance, Nile tilapia use chemosensory information to recognize conspecifics, thereby avoiding unnecessary aggression.[180] Additionally, when normally territorial catfish are exposed to water from the environment of other calm and non-aggressive catfish, they stop fighting.[181] Other species use a unique form of communication involving electric charges in which each species has distinct discharge patterns. In such species, both sexes are assisted in mate choice by deciphering the unique electric charge characteristic of his, or her, own species.[182]

Parental Behavior & Young Development

Parental care is not as widespread in fish as it is in other animal species: 78% of today's fish families are made up of species that do not practice parental care. Of the remaining 22%, species engaging in bi-parental care make up 32%. In fish families that dedicate only one parent to care of the young, males guard the nest in 50% while females are the sole protector in 18%.[183] Sargent posited that the likelihood of paternal care varies with the stage of the breeding season; males are much more likely to provide care in the middle and end of the season than at the beginning.[184] Furthermore, the sacrifice related to future fertility for fish providing parental care is greater for females than for males, therefore paternal care is more common.[185] However, in environments where females are much more prevalent than males, the incidence of nest abandonment by males may increase as a result of his future reproductive opportunities.[186]

Salmon & Trout

Unlike Pacific salmon, Atlantic salmon and many species of trout survive after spawning. Regardless of the parent's survival, salmonids show no other parental care beyond mate choice and the female's careful selection and preparation of the nest site.[187,188] Early stages of salmon and sea trout development are similar.[189] After approximately 70-160 days, depending on the water temperature, the alevins (newly hatched salmon or trout) emerge from their eggs in the spring. They remain in the gravel, where they have laid months earlier, for approximately three to four weeks while they rely on their attached yolk sac for sustenance. Once they emerge from the gravel as "fry", their yolk sac would have been absorbed and they must locate food to survive. After one year, the fry are known as "parr"; at this time they feed on insects and remain in their freshwater habitats for two to three years. Later, parr take on a silver coloration and are known as "smolts" in the spring of their second, third, or fourth year, depending on their environment. Once they become smolts, the fish begin their seaward migration, but offspring from one adult fish do not all journey to the sea in the same year or return to the stream simultaneously.[190] Much of their behavior at sea remains a mystery due to limitations of remote tracking systems in the open ocean. Some males have been observed foregoing their migration to sea and maturing in freshwater where they later attempt to engage in sneak fertilizations with adult females returning from the ocean.[191]

Bass

Male largemouth bass guard the nest and eggs during incubation. The nest may contain several hundreds to thousands of eggs, often contributed by a number of females.[192] Depending on the water temperature, eggs hatch after 5 days (80 °F) or 10 days (65 °F). Newly hatched fry remain in the nest while they absorb their yolk sacs, a process that can take one to two weeks. The male continues guarding the nest during this time, ceasing his vigilance as the fry leave the nest individually and yolk sacs absorbed after four to five days,[193] [194] when they are 0.5-1 inch in length. If the adult male is not in good condition prior to spawning, he may die once the fry leave the nest due to the stress of his protective role.[195] Pawson found that juvenile sea bass stayed close to the area of their birth throughout their first year. As adolescents they showed greater activity and traveled.[196] Adolescent striped bass have been observed gathering in large schools. However, little is known about larvae behavior, movement, and habitat needs for many species of bass.[197]

Tilapia

Cichlids are well-known for their extensive parental care and parent-offspring interactions. Because they rely much more heavily on complex systems of courtship, mating, and offspring protection, cichlids are less dependent on finding the perfect environment for their nest and offspring.[198] All species of tilapia build nests that are guarded by a parent. However, a number of species are mouth brooders in that they quickly take the fertilized eggs from the nest and incubate them in their mouth. Once they hatch, the young will often return to the parent's mouth for protection for several days. Depending on the species, males, females, or both participate in mouth brooding the young.[199] Solomon determined that in three cichlid species investigated, the adults could recognize their young among other offspring, most likely through chemosensory cues.[200] After the fry are mature enough to be released, the female remains in the area for several additional days to provide protection if necessary.[201] Tilapia fry are also observed forming schools while transitioning from parental care to independence.[202]

Catfish

Male channel catfish prepare and clean the nest site by fanning the substrate with their fins and bodies.[203] Once a male catfish has finished spawning and the female has released 2,000-70,000 eggs into the nest, he assumes protective duties and does not allow the female back to the nest as she may eat the eggs. As part of his protective duties, the male fans the eggs to help remove any waste released by the eggs, and he defends the nest aggressively.[204] In contrast, brown bullhead catfish *(Ameiurus nebulosus)* males share the guarding and parental duties with the female, typically protecting the nest and hatched young until they are approximately an inch long.[205] Once the eggs hatch, channel catfish fry stay in the nest for approximately a week before they begin schooling.[206] Flathead catfish *(Pylodictis olivaris)* eggs hatch after four to six days and engage in schooling around the nest area for several days thereafter. After leaving the school, fry initiate their independence by searching for cover under rocks or logs.[207] The same allegiance to the nest site during the first week of life is true for larvae of the Amazonian piramutaba.[208] In the Amazon basin, catfish juveniles are thought to migrate downstream from spawning sites in western Brazil's tributaries toward estuaries near the coast.[209] Interestingly, each species of predatory catfish has been found using different nursery areas, creating a geographic separation that may reduce competition.[210]

McKaye observed a rare phenomenon in fish: the parental feeding of young in Lake Malawi bagrid catfish *(Bagrus meridionalis)* in Africa. Young were observed gathering around the female's vent and consuming unfertilized eggs released by the female. Also, males were found returning to the nest with invertebrate food items for the young. Although the author conceded that there could be alternative explanations, he found strong evidence for his theory in the regular observations of catfish fry gathering and feeding around the male's gills following his return to the nest. This behavior has never before been seen in any fish species and likely increases the fry's growth rate and reproductive success of the parents.[211]

Intelligence

A variety of fish species have shown the ability to learn through classical conditioning. Salmonids learned to associate the arrival of food with a decrease in water temperature when the two were paired together over several trials.[212] Similarly, Reebs described Karl von Frisch's work in the early 20th century with a blind brown bullhead catfish who, after a few pairings of a whistle and a food reward, emerged from its shelter upon hearing the whistle.[213]

Imprinting, an important mechanism that facilitates survival in other young animals, is seen in fish as it relates to their natal stream. Many salmonids survive strenuous journeys to their natal stream for the purpose of spawning. Olfaction appears to be critical to this process, as young salmon that were removed from their natal stream early (as fry or parr) and placed into a different stream returned to the new stream whose smells and landmarks they recognized, instead of the one into which they originally hatched.[214]

Although social learning, or learning that is facilitated by observing conspecifics, has not been observed yet in salmonids, adult guppies have shown the ability to learn the path to a food source from another fish[215] as have French grunt, a coral reef fish.[216] As described earlier, goldfish are able to use the location and size of landmarks in relation to other objects in their environment to locate hidden food.[217] Atlantic salmon not only demonstrated their ability to use landmarks to find a reward, they also distinguished between two similar types of landmarks.[218] Reebs described Michel Anthouard's study in which juvenile sea bass who observed "knowledgeable demonstrators," or fish that had learned to push a lever to obtain food, learned to depress the lever sooner and used it more often than fish who observed individuals who had been unable to press the lever for food.[219]

Instrumental conditioning, when the frequency of a behavior increases or decreases depending on whether it is rewarded, has also been observed in fish. A number of species have been trained to push levers to receive a food reward, but researchers realize that there are limitations to what behaviors fish will perform for rewards due to their innate behavioral repertoire. For example, male sticklebacks cannot be trained to bite a rod to obtain access to a female because biting, or other aggressive behaviors, are instinctively inhibited upon sighting a female. Alternatively, they can be trained to swim or even jump through a ring to get access to a female, as these behaviors do not contradict their instincts.[220] Adron described the ability of rainbow trout to distinguish between a trigger that resulted in a food reward and one that did not, in a short period of ten days.[221]

Individual recognition is often associated with intelligence in animals, and a number of fish species appear capable of the task. A tropical anemone fish visually discriminates between its mate and other unknown fish by defending its anemone from all other fish except its mate.[222] Fry of many cichlid species discriminate between and prefer water that bears the odor of their mother and father, even though they may not prefer to be in the presence of their biological parents over other adults with young.[223] This is explained by the fact that fry from other cichlid adults are often accepted by unrelated cichlid parents as long as they are not significantly different in size from the adult's own offspring. Trout have also been observed displaying less aggression toward individuals with whom they had already met in dominance contests than those they had never been exposed to before.[224]Similarly, catfish showed signs of fear when exposed to water from a catfish that was dominant to them; however, they showed no such alarm when water from an unfamiliar catfish was introduced into their tank.[225]

Conclusion

Teleosts, or bony fishes, are the most plentiful and diverse vertebrate animals with more than 24,000 species alive today.[226] As such, they occupy extremely varied habitats and exhibit morphological rarities such as air-breathing organs and sensory systems capable of detecting subtle changes in water movement. Although a number of fish species have been studied in their freshwater life stages, further research on the behavior and habitat requirements of ocean-going fish is required. While fishes have historically been regarded as more "primitive" than other vertebrate groups, Rodriguez et al concluded that several memory and learning systems of bony fishes are noticeably similar to those of reptiles, birds, and mammals.[227] When animals as small and under appreciated as fish display complex mating systems, parental care, and demonstrate the ability to traverse significant distances using olfactory and celestial cues, it is clear that previously established definitions of intelligence should be revisited.

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