How fishes find their way around

Stéphan G. Reebs
Université de Moncton, Canada
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One of the joys of keeping fishes as pets is that you don't have to worry about them being unhappy because of confinement. Many fishes have a natural preference for small home ranges and they are quite satisfied with life in an ordinary aquarium (as long as you provide some objects for them to hide or swim around). This, however, does not mean that there isn't a need for proper spatial orientation in fishes. In nature, even a fish that spends all of its adult life within the boundaries of a small home range may occasionally get displaced by storms or by predators. After such misfortunes, the fish must be able to find its way back home, where the location of good food spots and hiding places is known. Moreover, large species, which are not very suitable for the pet trade and therefore not common in aquarists' living rooms, are often quite mobile in nature and may travel over wide areas. The seasonal migrations of salmon and other species are well known in that regard.[1]

Some fishes even embark on wide-ranging travels on a daily basis. In a study conducted in the Gulf of California by Peter Klimley and Donald Nelson, scalloped hammerhead sharks, *Sphyrna lemini*, were fitted with ultrasonic transmitters that allowed their movements to be tracked via receivers on boats. During the day the sharks were idling around a small seamount, but at dusk they left on foraging trips that took them as much as 8 km (5 miles) away, and yet at dawn they unfailingly returned to their point of departure.[2] Even more impressive are the journeys of one skipjack tuna, *Katsuwonus pelamis*, which was tracked by similar means off the island of Kauai in the Hawaiian archipelago. This fish could go as far as 35 km (22 miles) away from its usual resting place, and yet it always came back to that spot at the end of a foraging trip.[3]

Ultrasonic telemetry is useful in studies of this kind because the route taken by the homing fish can be plotted (more precisely, the route taken by the boat that follows the fish is plotted, but that works out to be pretty much the same thing). More information is thus available to figure out how the fish finds its way. Unfortunately, the technology also has drawbacks. The transmitters are expensive, have a lifetime of no more than several weeks, and are so bulky as to restrict their use to large fishes only. For fun, compare this to the 1950s' way of tracking fishes, a method that was low-tech and that still worked well for species living in lakes. Hooks were simply inserted through the dorsal musculature of a fish and attached to a small float via a long thread. The movement of the float at the surface would betray the movement of the fish below, and could easily be charted.[4] Imagine the surprise of boaters unaware of the ongoing study when they saw a piece of Styrofoam moving erratically on the surface of the lake!

More popular than telemetry or Styrofoam-tracking is the method of capture-displacement-recapture. In essence, this method consists of catching a fish in its home range (the area of which has already been determined by direct observations or by previous captures), tagging the fish, and then releasing it at a remote site. Traps are then set on the original home range, as well as elsewhere in the habitat, and this is done for many different individuals. If the displaced fish can find their way around, each one of them should get recaptured in the home traps and not elsewhere. However, if the fish cannot orient properly, recaptures should follow a random pattern in all traps.[5]

Through experiments of this kind, some impressive feats of homing have been documented. In New Zealand, Sue Thompson displaced mottled triplefins, *Forsterygion malcomi*, 700 m (that is roughly the length of 7 football fields) along the rocky reefs on which these fish lived. After 4-6 days, 8 out of 10 displaced triplefins had returned home.[6] This is not bad for a fish that is only 7-10 cm (3-4 inches) long and that spends all of its adult life on territories that are only 2 m^2. Similar results have been obtained with radiated shannies displaced over 270 m,[7] flathead catfish over 1 km,[8] cardinalfishes over 1-2 km,[9] various sunfishes and bass over 3.5 km,[10] and yellowtail rockfish over 22 km.[11]

All of this brings us to the key question: How do fishes find their way back home? A first possibility is the existence of internal compasses. These can be based on sun position, polarised light fields, magnetic fields, or electrical fields. Olfaction may also play an important role in home-finding: fishes could be drawn by the smell of their home. Finally, visual landmarks can provide beacons for orientation. As this list suggests, fishes can resort to a number of different mechanisms to find their way around, and we should bear in mind that these mechanisms are not necessarily exclusive of one another.

Sun compass

Most people are familiar with the notion that, with a watch and a view of the sun, it is possible to infer the position of any cardinal point. The sun is always over the east in the morning, over the south at midday (north in the Southern Hemisphere), and over the west at the end of the day. Points in between can be interpolated. Because fishes have an internal (circadian) clock that allows them to estimate the time of day, they can use the position of the sun to infer cardinal directions.[12]

Classical tests go like this: first, a fish is placed inside a container in the middle of a circular pool. The surroundings are uniform except for a view of the sun, or at the very least a bright lamp that moves around like the sun. The pool itself is as uniform as possible, and it is regularly rotated to prevent the fish from learning to rely on small landmarks inside the pool that might not be perceivable by people. All around

the periphery of the pool are a number of identical shelters or feeding stations, depending on the motivation of the fish at the moment of the test (finding shelter or finding food). They too can be rotated regularly. It is assumed that the fish always wants to go in the same cardinal direction, either because it does so in nature (some fish, for example, go offshore to feed and inshore to take shelter, and these represent constant directions throughout the life of a fish whose home range remains the same), or because the individual has been previously trained by the researcher to always go in the same direction (for example, of all the shelters around the periphery, only the one to the south-east is open).

So, the fish is released from the central container and the direction in which it swims is noted. If the fish can use sun-compass orientation, it should always swim in the correct direction, no matter what time of day it is, just as long as the sun (or lamp) has moved around the pool at a natural rate. Machiavellian researchers can also hide the true position of the sun and use mirrors to deflect its apparent position by, say, 90°, with the expectation that the preferred direction of the fish would also shift by 90°. Another variant is to test the fish with and without a view of the sun (on sunny and cloudy days, for example) with the expectation that correct orientation would be lost when the sun is not visible.

With these methods, sun-compass orientation has been demonstrated in at least a dozen species of fish: white bass,[13] pumpkinseed sunfish,[14] bluegill sunfish,[15] green sunfish,[16] largemouth bass,[17] Southern starhead topminnow,[18] sockeye salmon,[19] mosquitofish,[20] two cichlids (*Cichlaurus (=Heros?) severus* and the uaru),[21] one characid,[22] and two parrotfishes (the purple and the rainbow parrotfish).[23] In at least one of those studies, the contribution of the internal circadian clock was convincingly illustrated. Phillip Goodyear and David Bennett, then at the Savannah River Ecology Laboratory in South Carolina, captured immature bluegill sunfish that were in the habit of moving in a known direction to reach their natural refuge. When tested in a circular pool at midday in full view of the sun, these fish oriented correctly, equating the sun position with a southerly direction and moving appropriately relative to that. But Goodyear and Bennett also kept some fish in the lab under a photoperiod that had been advanced by 6 h (the fish "got up" at 1 AM instead of 7 AM). When these fish were tested under the natural midday sun, they did not orient as if the sun was over the south. Instead they interpreted the sun position as being west.[24] Their clock, which had been advanced along with the artificial photoperiod, told them they had been up for 11 hours and that this was the end of the day, and every decent fish knows that the sun is over the west at the end of the day! These results clearly indicated that fishes do not use sun height or even light colour as temporal cues, but sun position and the counsel of their internal clock instead.[25]

Sun-compass orientation has some limitations in aquatic environments. Objects that are low over the horizon cannot be seen from within the water, because of the reflection of light rays at the water surface. The sun, therefore, cannot be viewed by fish around dawn and dusk. Moreover, the sun disk can be hidden by clouds and,

even if it is not, its precise position remains hard to establish from depths of more than a few meters. Some attention has therefore been devoted to indirect means of detecting the sun's position, means that overcome the above limitations. If fact, there is only one good possibility for this, and it is the ability to perceive and orient to the pattern of light polarisation that is present in the sky. The alignment of this polarised light field varies predictably with the position of the sun, can be seen from depths of 200 m or more (albeit in reduced intensity), and can be seen in open parts of the sky even when the sun disk itself is low over the horizon or obscured by clouds.[26]

While he was at McMaster University in Hamilton, Ontario, Craig Hawryshyn tested the ability of rainbow trout to orient to polarised light. He and his co-workers first created a polarised light field by fitting linear polarising filters to a tungsten-halogen projector hanging from the ceiling. Then they placed a long rectangular aquarium parallel to the axis (the so-called "e-vector") of that light field, and trained trout to swim along this pathway to reach a shelter at the end. Then, in the same light field, they set up a circular wading pool, released the trained trout in the middle of it, and noted the direction in which the fish swam. The majority of the trout still moved parallel to the field vector, even though the circular pool now allowed them to go in any other direction. The experiment worked again when other fish were trained to swim perpendicular to the vector rather than parallel to it. These fish maintained the learned perpendicular orientation when tested in the circular pool.[27] Obviously, for them to do this, they had to be able to perceive the orientation of the polarised light field.

Such results indicate that fishes may be capable of using a polarised light compass (or, in other words, a sun compass with an indirect means of pinpointing sun position). However, the true usefulness of such a compass in nature is still uncertain. The Hawryshyn team has also shown that polarised light detection requires the presence of UV-sensitive cones in the retinas of the trout, and these cones may be lost when the fish become adult. Indeed, in the above experiments the researchers could not get adult trout to orient properly, only immatures of less than 30 g. The use of polarised light compasses may therefore be restricted only to those fish species that can perceive UV light. A further limitation resides in the progressive degradation of the polarised light field as depth and turbidity increase. In a subsequent study by Hawryshyn, less than 20% of tested trout oriented properly under a field that was only 65% polarised.[28] Therefore, even though polarised light can be detected at great depth, its poor quality there may prevent its use as a spatial cue. The topic of orientation by polarised light needs to be further studied, preferably under the natural sky.

Magnetic and electric compasses

We are familiar with the magnetic compass, the kind we use when we go on backcountry hikes. The magnetized needle points north. A similar mechanism can be

used by animals.[29] Magnetite particles, Fe_3O_4, which can form the core of biological magnetic receptors, have been found in the head of salmon [30] and inside specialised cells within the nose of trout.[31] These cells were found to be connected to the brain by a special nerve, and signals were detected on this nerve when the fish perceived magnetic anomalies in their environment. Fishes in fact represent the first vertebrate for which such potential magnetoreceptors *and* associated neurological hardware have been identified.[32]

This anatomical evidence is rather recent, and researchers did not wait for it to prove that fishes could maintain their bearings in a magnetic field. Protocols for this task were simple enough, although they necessitated the use of equipment capable of creating artificial magnetic fields or modifying the natural one. Once so equipped, all that was left to do was to obtain fish that showed a consistent orientation in a magnetic field – either naturally or because they had been trained to do so – and then alter the field. One expectation was that the initial orientation would disappear if the magnetic field was abolished. And if the magnetic field was experimentally rotated, the prediction was that the preferred orientation of the fish would also rotate. In many cases, such predictions were upheld.

Lincoln Chew and Grant Brown, at the University of Lethbridge, Alberta, put commercially-bred rainbow trout in circular arenas, and found that these fish repeatedly (but unexplainably) faced towards the magnetic north. The trout were not lining up with spatial cues from outside the pool because the visible surroundings were regularly moved between trials, and yet the fish still faced north. However, when the experiment was repeated in a room enclosed in Mu-metal (a special nickel-silver alloy) and lined with grounded copper strips to eliminate the natural magnetic field, the orientation of the trout became random.[33] Similar results have been reported in leopard sharks, *Triakis semifasciata,* which also, intriguingly, oriented in a northerly direction when placed in a normal magnetic field.[34]

At the University of Auckland in New Zealand, P.B. Taylor kept introduced Chinook salmon in a rectangular tank oriented east-west, with the water flow and the food coming from the west. The fish, understandably, faced west. Things got more interesting when the salmon were moved, 18 months later, to a circular tank in another location without a view of the sky but within a normal geomagnetic field. Even though the water flow was not directional any more, the fish still faced west. Taylor installed Helmholtz coils (circular wraps of copper wire energised by a DC power supply) around the arena and, by turning on the power in the appropriate coils, eliminated any trace of a magnetic field. The orientation of the fish became random. In other trials, the coils were realigned so as to preserve the local magnetic field, but rotated 90° clockwise. The fish's orientation also changed by 90°, but either clockwise or counter-clockwise (they faced north or south instead of west).[35]

Because the salmon in the shifted field faced either north or south rather than north only, their behaviour was called alignment rather than orientation. There is no solid

explanation for this quirk of behaviour. Perhaps alignment results from an imperfect detection of the magnetic field polarity. At any rate, alignment seems to be peculiar to magnetic orientation. It is not seen in other types of compass. This is illustrated by the work of Thomas Quinn and Ernest Brannon from the University of Seattle, who studied the migration behaviour of juvenile sockeye salmon in Babine Lake, British Columbia. This lake is 150 km long and lies along a northwest-southeast axis. At the time of their capture, the young smolt studied by Quinn and Brannon were intent on leaving the lake on their seaward journey. When tested in circular arenas, they oriented properly in one direction: towards the outlet of the lake in the northwest. This, however, happened only when they had a clear view of the sky, and at such times their performance was not affected by the orientation of the magnetic field (normal or rotated 90° counterclockwise). However, when opaque covers were draped over the arenas to mask the view of the sky, the fish started to orient both towards and straight away from the outlet, and they readjusted this alignment accordingly when the magnetic field was rotated.[36]

These findings first reveal a hierarchy of compasses, with the visual compass having priority over the magnetic one. When the sun is visible, only the sun compass is used, and proper orientation without alignment is achieved. When the position of the sun cannot be established, the fish is forced to rely on the magnetic compass, and alignment rather than complete orientation is the result. This is rather bad for those fish that end up facing away from the outlet of the lake, but perhaps they can eventually use other cues, such as water currents,[37] to realise the error of their ways.

Another, more esoteric kind of compass is an electrical one. Several fish species can detect electrical fields. In one experiment, a circular tank was set up with electrodes at 90° intervals along the periphery. When a pair of diametrically-opposed electrodes was activated, a DC current passed uniformly through the tank. In this arena, brown bullheads, *Ameiurus nebulosus*, were trained to swim from a central shelter to a feeding station 45° to the right of the negative electrode, a task they learned quickly. Now, when the electrodes were suddenly switched off and the other pair was turned on, the catfish searched for food 45° to the right of the newly-active negative electrode, not the previous one.[38] Electrical compasses are therefore a reality, at least in catfish. Whether this means of orientation is useful to catfish in nature would depend on the existence of steady voltage gradients in their environment. Such hydroelectric fields have indeed been measured in some ponds and streams.[39]

Use of olfaction

All compasses, be they visual, magnetic, or electrical, provide only partial information. They inform fishes about the heading that should be followed in order to get home, but not the precise location of home. If a sunfish, for example, learns through regular short-range excursions that its home is on the eastern shore of a lake, then after a long displacement it can use its compass and head east until it hits the

shore. Once there however, it may still have to swim up and down the shoreline at random before it finally stumbles upon its familiar surroundings. This could take time, especially if the eastern shore is a long straight one. Similar scenarios can be imagined for coastal species. Are there any other tricks the fish can resort to so as to facilitate their task once their compass ceases to be useful?

A good mechanism would be to cue in to the smell of the home area. Such a smell would normally radiate in all directions if there is no current, or it would form a plume downstream if there are currents. Upon hitting a familiar smell, the fish could be induced to swim up the gradient of odour, or up current if there is one, until it finds the visual landmarks or the normal odour concentration of its home area. This idea assumes that the home area is endowed with a different odour than all other regions, that fish can learn this odour, and that their sense of smell is good enough to detect it even at very diffuse concentrations.   All of this would be proven if anosmic (smell-impaired [40]) fish could be shown to have reduced homing success as compared to normal individuals. Several studies have in fact managed to do this.

On the west coast of Vancouver Island, Hong Woo Khoo, a PhD student in the laboratory of Norman Wilimovsky at the University of British Columbia, studied the homing capacity of the tidepool sculpin, *Oligocottus maculosus*, within its intertidal habitat. He captured many individuals from their home pools and made some of them anosmic by cauterising the inside of their nose while leaving the other fish untouched. Then he displaced all of them up to 125 m along the shoreline. Less than 8% of the smell-impaired fish found their way back to the home pool, versus 20-80% – depending on the experiment – for the intact fish. The poor success of the anosmic fish was not caused by post-operative shock, because other sculpins were also subjected to surgery, this time to make them blind, and these blind fish homed almost as well as the controls. They could still smell, and that seemed to be the key.[41]

In a similar experiment, Morten Halvorsen and Ole Stabell from the University of Tromso in Norway displaced brown trout 200 m upstream or downstream from their home site. Beforehand, they had anaesthetised the fish and cauterised the olfactory detectors of some of them while cauterising two sites near the nasal openings of the others (this latter procedure did not make the fish anosmic but provided a control for the possible shock of operation and handling). More than four times as many control fish came back to their home within the next 9 weeks as compared to the smell-impaired individuals. Interestingly, the controls that had been displaced upstream, where they could not smell home, came back just as successfully as those that had been moved downstream. We can therefore imagine that, within a stream habitat, displaced fish could follow a rule of thumb such as "If you can smell home, swim against the current, but if what you smell is not like home, then swim with the current until you do smell home". Most of the anosmic trout were recaptured around their site of release, so maybe their rule of thumb was "If you can't smell anything, stay put".[42]

It is a short jump from trout to salmon, which portray the classical example for the importance of olfaction in homing behaviour. When they are young, salmon learn the smell of the stream in which they live. Later, they leave the stream to go live at sea. Much later still, they come back to their natal stream in order to spawn in it. These adult salmon find their natal stream by following their nose – the trail of the odour learned several years earlier but not forgotten. The main player in the research that elucidated the mystery of this homing mechanism is Arthur Hasler from the University of Wisconsin. The time frame is the 1960s and 70s. Hasler's first experiment followed the now familiar protocol of catching adult salmon, making some of them anosmic (by plugging their nostrils) while leaving others untouched, and measuring their respective success at returning to the stream where they had been born and originally tagged. As you can guess, fish with unplugged noses made it home successfully whereas the anosmic ones were recaptured more or less evenly among all of the streams of the basin. The point was driven home (along with the fish) in a subsequent series of elegant experiments. Hasler and his co-workers reared young coho salmon in a hatchery and exposed them to one of two different chemicals, morpholine and phenethyl alcool (PEA). These artificial chemicals do not normally carry biological meaning but they are odoriferous. The fish were then marked according to the chemical they had been exposed to, and released into Lake Michigan. During the spawning migration 1.5 years later, the researchers dripped morpholine into one river and PEA into another 9 km away. Convincingly, 95% of the fish that were recaptured and that had been exposed to morpholine were recovered in the morpholine-scented river, and 92% of the recaptured PEA fish were recovered in the PEA-scented stream. One cannot ask for a better experimental demonstration of the importance of odours for homing salmon.[43]

We still do not know the nature of the chemicals that provide the odour learned by fishes in the wild. Geosmin, a chemical produced by tiny mushrooms and present within inland waters, is a possibility. Glass eels have been shown to detect it and to prefer water laced with it at a time when they want to migrate into rivers.[44] Another intriguing possibility is that the smell of other fish might contribute to the olfactory "bouquet" of the home stream.[45] Experiments have revealed that salmon can distinguish between the smell of conspecifics from their own population versus that of others.[46] One of these experiments showed that Arctic char which were reared in hatcheries with some of their brothers and sisters, the smell of which could therefore be memorised, preferred, once released in the wild, to ascend the river where other relatives were present.[47] So maybe adult salmon migrating upriver could seek the smell of the juveniles presently living in their natal stream, assuming that these adults and juveniles all share an ancestral olfactory signature.

Many coral reef fishes go through a drifting larval stage before settling down on a patch of coral. A number of studies have shown that the presence of other residents on coral heads can influence the probability that larvae will settle there. In one field study conducted by Hugh Sweatman on the Great Barrier Reef of Australia, water was pumped at night from coral heads with and without resident humbug damselfish,

Dascyllus aruanus, into similar but unoccupied coral patches. The larval fish that settled through the night on these scented patches were collected at dawn by spreading the anaesthetic quinaldine over the coral. At the sites supplied with humbug-occupied coral water, many larvae of the humbug damsels had settled. At the sites supplied with unoccupied coral water, fewer larvae had settled. Sweatman concluded that the odour of adult conspecifics acts as an attractant in the settlement behaviour of larval humbugs. He pointed out that chemical information may be important for all species, such as humbug damselfish, that settle at night and cannot visually inspect their prospective real estate.[48]

Some experimenters have reported that larval coral fish, once released at night in open waters 1 km away from the nearest reef, unerringly take off in the direction of that reef. Perhaps they follow an odour plume emanating from the reef. A recent study has found that the larvae of two coral reef species – the spiny chromis *Acanthochromis polyacanthus*, and a cardinalfish – can distinguish between water from their own natal reef and water from a foreign reef, showing a preference for the natal reef water. Whether the relevant odour comes from the reef itself or from its occupants is unknown. [49]

Use of sounds

The idea has also been put forward that larval coral fish use sounds made by crashing waves and by the adult fish already on the reef as a directional cue.[50] Some evidence for this was provided in 2005 when a paper in Science magazine reported that more fish larvae – mostly cardinalfishes and damselfishes – settled on reefs on which speakers broadcasting sounds of snapping shrimp and fish calls had been installed, as opposed to "silent" reefs.[51]

Use of landmarks

A final possibility for orientation is the recognition of landmarks. [52] While it seems likely that familiar landmarks are used by fishes for home range recognition,[53] their usefulness for long-distance orientation is more doubtful given the limited visibility that can be achieved in water. But for some type of short-distance movement, landmarks could be helpful. The behaviour of the small frillfin goby *Bathygobius soporator* is interesting in that respect. These fish live in the intertidal zone and at low tide they are confined to tide pools. If they are chased by mad scientists while in such a pool, they jump out of the pool and "land", with amazing accuracy, in adjacent pools! Sometimes they jump from pool to pool until they reach open water, a trip that may require up to 6 different jumps, not all of them in the same direction. This works only when the fish have had a chance to explore the whole area at high tide, when all pools are covered by water and swimming between them is possible. When introduced into an unfamiliar pool at low tide, gobies refuse to jump or they jump

wrongly onto rocks. But after only one night of exploring around that new pool at high tide, the jumping behaviour becomes accurate again. This is true even under cloudy skies, which shows that a sun compass is not used. There is still the possibility of a magnetic compass at work, but the most likely hypothesis is that the shape of each pool is memorised and serves as the main cue for proper orientation towards the next landing place.[54]

Fishes could also learn the order of a series of landmarks and establish routes along them. Many coral reef fishes move off the reef on their way to feeding areas at dawn and back along the same route at dusk. Every day, the same route is used. Divers who have observed this behaviour could not help but reflect that the fish were following a series of specific landmarks. Supporting this idea, individual butterflyfish that were experimentally displaced off the route seemed to move at random at first, but as soon as they happened to cross their well-known path, they turned and went straight home along it, as if recognizing it.[55] Unfortunately, observations of this kind do not provide information about the exact nature of the specific landmarks. To learn more, one would have to remove some of the possible landmarks. Such a task would be made difficult by the fact that relatively large areas of sand or rock might be used as signposts. These would be hard to remove!

Whatever the mechanism or species involved, successful homing by animals inspires awe in anyone who witnesses it – and witness it we can if we take the time to sit by a tide pool and recognise the same sculpin in it, or by a turbulent stream and admire the efforts of a salmon ascending it. There is more than a little mystery about the art of not getting lost, but a good part of it has been made less puzzling by patient research. This field of investigation is difficult, and therefore stimulating for some, because it requires broad knowledge in sensory physiology (vision, olfaction, electroreception, magnetoreception), chronobiology (circadian clocks), and physics (magnetic fields, celestial movement), not to mention expertise in the capture and tagging of wild animals. But even knowing how fish succeed in homing does not make the feat less awesome, as the mechanisms themselves turn out to be exquisitely complex. They are also remarkably efficient in the face of the aquatic environment's vast expanses.

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[1] For more examples of fish migrations, and for a general review on the topic of spatial orientation in fishes, see: Quinn, T.P., and Dittman, A.H., 1992, Fishes, pp. 145-211 in: Animal Homing (F. Papi, ed.), Chapman & Hall, London; R.J.F. Smith, 1985, The Control of Fish Migration, Springer-Verlag, Berlin; Dodson, J.J., 1988, The nature and role of learning in the orientation and migratory behavior of fishes, Environmental Biology of Fishes 23: 161-182. For recent specific examples of migratory feats, see: Hunter, E., Metcalfe, J.D., and Reynolds, J.D., 2003. Migration route and spawning area fidelity by North Sea plaice, Proceedings of the Royal Society of London B (Biological Sciences) 270, 2097-2103; Quinn, T.P., Stewart, I.J., and Boatright, C.P., 2006, Experimental evidence of homing to site of incubation by mature sockeye salmon, *Oncorhynchus nerka*, Animal Behaviour 72, 941-949; Block, B.A., Teo, S.L.H., Walli, A., Boustaby, A., Stokesbury, M.J.W., Farwell, C.J., Weng, K.C., Dewar, H.,

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[5] Displacement protocols also have drawbacks. Some fish may lose their tags, unless fin-clipping is used as a marker. Some fish may return home but not be recaptured because they have learned to avoid traps. Some fish may fail to return home but only because they were caught by predators, not because of a lack of homing capacity. Some fish may judge the site of release to be better than their home range and decide to stay there. And no information is obtained on the route taken to get back home.

[6] The 10 fish were all males. A replicate with 10 females yielded only 1 successful return at 700 m. The difference remains unexplained, although it disappeared at shorter distances (males and females homed equally well from 200 m away) and at longer distances (neither males nor females could home from 2 km away). Thompson, S., 1983, Homing in a territorial reef fish, Copeia 1983, 832-834.

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[12] If the fish does not use an internal clock (if the orientation mechanism is not time-compensated), then orientation is still possible but it is limited to the times of sunrise (the sun is reliably in an eastern direction) and sunset (the sun is over the west). This works well for species that carry out daily migrations at dawn and dusk and that live in generally sunny climes. See : Gruber, S.H., Nelson, D.R., and John F. Morrissey, 1988, Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon, Bulletin of Marine Science, 43, 61-76.

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