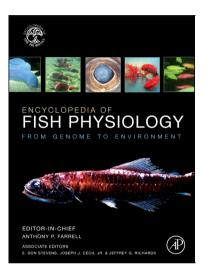
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# PHYSIOLOGICAL SPECIALIZATIONS OF DIFFERENT FISH GROUPS

### **Fish Migrations**

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### The Biology of Fish Migration

TR Binder, Hammond Bay Biological Station, Millersburg, MI, USA

SJ Cooke, Carleton University, Ottawa, ON, Canada

SG Hinch, University of British Columbia, Vancouver, BC, Canada

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#### Glossary

**Amphidromy** An uncommon subcategory of diadromy, in which there is a brief excursion from freshwater to seawater during the juvenile stage, but the majority of feeding and growth and spawning occur in freshwater.

**Anadromy** Life-history strategy entailing reproduction and early rearing in freshwater followed by a significant growth phase in seawater.

**Catadromy** A subcategory of diadromy, in which the majority of feeding and growth occurs in freshwater and the fully grown adult fish migrate to saltwater and reproduce.

**Crepuscular** Occurring during twilight (dusk and dawn). Daily pattern with two peaks of activity centered around dusk and dawn, though not excluding some activity in between these periods. From Latin 'crepusculum' (twilight).

**Diadromy** A category of migration, in which all migratory activity crosses the seawater/freshwater boundary.

Diel Pertaining to a 24-h period.

**Fluvial** Relating to a river, stream, or other flowing water.

**Iteroparity** A reproductive strategy whereby an individual reproduces more than once within its lifetime. **Lateral line** Sensory structure consisting of a series of mechanoreceptor cells on the surface of the body of fishes and for detection of water motion relative to the body and low-frequency sound.

**Migration** A regular directed movement of a group of animals.

**Navigation** A mechanism whereby fishes plot a course to a particular location.

**Oceanodramy** A category of migration, in which all migratory activity occurs in saltwater.

**Orientation** A mechanism whereby fishes position themselves in a particular direction in response to an external stimulus.

**Potamodromy** A category of migration, in which all migratory activity occurs in freshwater.

**Rheotaxis** A directional preference to flowing water. **Semelparity** A reproductive strategy whereby an individual reproduces only once within its lifetime.

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#### What is Migration?

It is sometimes the case in fishes that the life history needs of a population (e.g., foraging and reproduction) cannot be met by a single habitat. This is due to variability in the habitat conditions (e.g., temperature), or to the changing needs of the population itself (e.g., foraging habitat vs. spawning habitat). In such cases, the fitness of individuals benefits from movement to an alternate habitat. As a result, many fishes have evolved a life history that includes coordinated movement from one habitat to another. This synchronous, directed movement of part or all of a population between discrete habitats is called 'migration'.

Approximately 2.5% of all fish species undertake migrations. The physical scale of migrations is highly variable and can range from hundreds of meters, as in some coastal and stream dwelling fishes, to thousands of kilometers, as in eels (Anguilla spp.; see also Fish Migrations: Eel Migrations) and tunas (Thunnus spp.; see also Fish Migrations: Tracking Oceanic Fish). The timing of migration typically occurs on a seasonal scale, though some species display coordinated daily movements (e.g., vertical or tidal migrations). According to some authors, this represents migratory activity and, to others, these movements are a specialized form of foraging. In this article, we focus on longer-distance migrations, not because short-distance and vertical migrations are ecologically or evolutionarily less important, but because long-distance migrations typically impose greater behavioral and physiological challenges on fishes than short ones.

#### **Classifying Migrations**

Fish migrations are typically grouped into three categories, based somewhat arbitrarily on their relationship to the seawater/freshwater boundary (**Figure 1**).

- 1. Oceanadromous migrations, such as those performed by tunas, white sharks (*Carcharodon carcharias*), and plaice (*Pleuronectes platessa*), occur entirely within seawater.
- 2. Migrations that occur entirely within freshwater are classified as potamadromous. Potamadromous migrations can occur solely in lakes (e.g., lake trout, *Salvelinus namaycush*), in rivers and streams (e.g., brook lampreys, *Lampetra* spp.), or can span both lake and fluvial habitats (e.g., white suckers, *Catostomus commersoni*).
- 3. Migrations that cross the seawater/freshwater boundary (e.g., Pacific salmonids, *Oncorbynchus* spp.) are classified as diadromous. There are three subcategories of diadromy – anadromy, catadromy, and amphidromy:



**Figure 1** Map of the northeast coast of North America displaying example migratory patterns for the three major categories of fish migration. Migrations are categorized based on their relationship to the seawater/freshwater boundary – see text for details. Sources of map image: http://oversights.org.uk/.

- (a) Anadromy occurs when most feeding and growth occurs in saltwater and fully grown adults move back into freshwater to spawn (e.g., Pacific salmon).
- (b) Conversely, catadromy occurs when most feeding and growth occur in freshwater and the fully grown adults move into saltwater to spawn (e.g., eels).
- (c) The last subcategory, amphidromy, occurs when there is a brief excursion from freshwater to seawater during the juvenile stage, but the majority of feeding and growth and spawning occurs in freshwater. This last subcategory is most common in fishes inhabiting islands in the tropics and subtropics (e.g., sicydiine gobies, *Sicydium* spp.)

While it might be convenient to classify migrations, the above categories and subcategories do not provide any insights into the behavioral or physiological challenges involved in migrations, with the notable exception that diadromous migrants must contend with an osmoregulatory challenge as they move between the freshwater/ seawater environments (see also Osmotic, Ionic and Nitrogenous-Waste Balance: Osmoregulation in Fishes: An Introduction). As a result, this article focuses on the requisite properties for long-distance migration, rather than their categories.

#### **Orientation and Navigation**

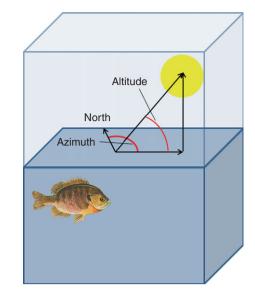
There is a long history of interest in orientating and navigating mechanisms in fishes that stems from the discovery in the 1930s that salmon return from the ocean to their natal streams to spawn (termed 'homing'). Since then, homing has been demonstrated for numerous fish species. Originally, it was believed that the phenomenon involved a spectacular navigation mechanism. However, despite intensive research on the mechanisms of homing in fishes, no precise navigation ability has yet been demonstrated. This prompted researchers to test the hypothesis that homing is accomplished through random search. Not surprisingly, a random search model alone was insufficient to explain homing in salmon. However, when slight directional bias (orientation) was added to the model, the predicted return rate was similar to the observed return rate for these fish.

Several orienting mechanisms have been proposed, and it is likely that several different cues might be involved in orientation at various stages of migration. In particular, orientating behavior differs markedly between open water and fluvial migrations. In open water, fishes may migrate in any one of 360° of direction. By contrast, fluvial migrants are confined within a relatively narrow channel plus they have the added cue of migrating either with or against the current, termed negative or positive rheotaxis, respectively. Because of this dichotomy, we discuss the possible orienting mechanisms for open water and fluvial migrations separately.

#### **Orienting in Open Water**

Stemming from pioneering work by Hasler in the late 1950s, there is now considerable evidence that fishes use solar cues to orient during open water migrations. Fishes may orient using information derived from changes in the sun's azimuth (angle of the sun in the horizontal plane) and/or altitude (angle of sun in the vertical plane) (Figure 2). However, because these measures change on both a diel and seasonal scale, fishes that orient using the sun must possess an internal biological clock and calendar to compensate for these changes. For salmon that spawn on very precise dates of the year, the idea of an internal biological clock is not an unreasonable expectation. Indeed, laboratory experiments in a variety of species have demonstrated that fishes may be trained to use an artificial sun to orient in a particular compass direction. Moreover, fishes trained to orient in this manner can correctly compensate for diel and seasonal variation in the position of the sun.

The sun itself is often obscured and, thus, is not always a reliable orienting cue. Nonetheless, fishes may continue to orient when the sun is obscured by using polarized light as a directional cue. The ability to detect and discriminate planes of polarized light has been demonstrated in numerous species. However, there is some evidence that polarized light would be a reliable orienting cue only during crepuscular periods (dawn and dusk) when the percentage of polarized light is as high as 60–70%. During the day, the percentage is far lower (<40%), and



**Figure 2** Solar information used by fishes for orientation in open water. Directional information is derived from changes in the angle of the sun in both the vertical (altitude) and horizontal (azimuth) planes. Fish possess a biological clock and calendar that allows them to compensate for diel and seasonal changes in these parameters.

may in fact be below the detection threshold of most fishes.

There is a growing body of support for geomagnetic orientation, particularly in fishes such as Pacific salmon and eels (see also Fish Migrations: Eel Migrations), which undergo long-distance oceanic migrations. When water moves across the Earth's magnetic field, it induces a weak electric current that may be detected by fishes. In rainbow trout (Oncorbynchus mykiss), changes in the intensity of the Earth's magnetic field are detected by discrete magnetoreceptor cells located in the olfactory epithelium. These cells, which contain chains of magnetite crystals (biogenic Fe<sub>3</sub>O<sub>4</sub>) that transduce the induced electric current into a sensory signal, are innervated by a branch of the trigeminal nerve. There are, however, opponents to the theory of geomagnetic orientation in migrating fishes. The two main arguments against this type of orientation are that: (1) temporal and spatial variations in the magnetic field would make it difficult to form a useful magnetic map; and (2) there is as yet no evidence that fishes possess the ability to memorize such a map, even if they were capable of forming it (see also Sensory Systems, Perception, and Learning: Magnetic Sense in Fishes). Nevertheless, salmon can memorize the complex odors of a natal stream for their entire seaward migration, which can last several years.

The tendency to orient in a current is called rheotaxis. In open water, large-scale currents substantially influence the direction and speed of some migrations. For example, the ocean migration pattern of Pacific salmon from British

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Columbia (Canada) is largely determined by interannual variations in the strength of the Alaskan Gyre, a counterclockwise current in the Gulf of Alaska. Smallerscale currents can also be important. For example, models of the migratory behavior of Pacific salmon that encounter the Sitka Eddy (mesoscale eddy located northwest of the Queen Charlotte Islands, BC, Canada) suggest that salmon can exploit the rotational current of the eddy to increase speed and moderately reduce the energetic costs of migration. More recently, it has been hypothesized that even subtle currents may be important during the open water phase of migration of salmon to their natal streams.

Differences in water temperature and salinity create vertical layers and each layer has a distinct origin, presumably with its own unique home stream 'olfactory bouquet', which plays a dominant role during the final stages of locating the natal stream (see also Fish Migrations: Pacific Salmon Migration: Completing the Cycle). Behavioral studies have shown that both Pacific and Atlantic salmon tend to migrate within a single vertical layer, but make brief periodic excursions into adjacent layers. Salmon may use these excursions to determine the direction of the layer's origin by detecting the acceleration that occurs as they cross between adjacent layers. It is unlikely that the lateral line is sensitive enough to detect the subtle differences in velocity between adjacent layers. However, the otolith organs are capable of detecting minute accelerations and, depending on how quickly the fish move between adjacent layers, could be capable of detecting velocity differences as small as  $1 \text{ mm s}^{-1}$ .

#### **Orienting in Fluvial Habitats**

Navigation in fluvial habitats is less complicated than in open water. Here, water current is the primary orienting cue - migration is the result of the tendency of animals to orient with the current (negative rheotaxis) or against it (positive rheotaxis). Studies that employed a combination of Co<sup>2+</sup> and aminoglycoside antibiotics (streptomycin and gentamicin) to block various components of the mechanosensory lateral line system have demonstrated that the lateral line is involved in mediating rheotactic behavior. Specifically, a single class of lateral line organs located on the surface of the skin, superficial neuromasts, appears to be important. A second class of lateral line organs, canal neuromasts, are located within canals beneath the surface of the skin and may contribute to navigation in complex flows (see also Hearing and Lateral Line: Lateral Line Neuroethology). Nevertheless, the lateral line is incapable of mediating rheotaxis on its own. Rheotaxis depends on a fixed frame of reference from which the fish can determine both the speed and direction of flow. This is accomplished using either visual cues or through periodic contact with the substrate.

There is overwhelming evidence that olfactory orientation is an important component of navigation in fluvial migrants. The olfactory basis of upstream migration has been most extensively studied in Pacific salmon and sea lampreys (Petromyzon marinus). Upstream-migrating salmon home to a stream-specific set of olfactory cues that are imprinted prior to their emigration from the stream as smolts (see also Fish Migrations: Pacific Salmon Migration: Completing the Cycle). In sea lampreys, the situation is somewhat different. Spawning phase sea lampreys do not home to their natal stream. Instead, they are drawn to streams with suitable spawning habitat by a multicomponent bile acid pheromone released by larval lampreys, which they can detect at extremely low concentrations (see also Hagfishes and Lamprey: Lampreys: Energetics and Development and Lampreys: Environmental Physiology). Interestingly, while these navigation strategies differ significantly, the mechanism by which olfaction mediates upstream migration appears to be the same.

The general consensus is that olfactory cues induce upstream migration in fishes through olfactory-mediated rheotaxis. This conclusion is based on two main observations. First, fishes tend to display significantly greater upstream activity (positive rheotaxis) when the correct olfactory stimulus is present than when it is not. Second, upstream migrants that no longer detect the olfactory stimulus, such as when the stimulus is pulsed, the animal is anosmic, or when the animals pass upstream of the stimulus source, display significantly greater movements in the downstream direction (negative rheotaxis). Downstream migrations, like those of salmon smolts, could similarly be induced by olfactory-mediated rheotaxis in response to conspecific olfactory cues. However, there is as yet no experimental evidence to support this assertion (see also Sensory Systems, Perception, and Learning: Spatial Orientation: How do Fish Find their Way Around?). Clearly, aquatic pollutants that impair olfaction (see also Toxicology: The Effects of Toxicants on Olfaction in Fishes) could have catastrophic effects for these fishes.

#### **Energetics of Migration**

Long-distance migrations, especially upstream migrations in fluvial systems, are energetically demanding, and feeding during long-distance migrations is rare. The reason for this is that feeding imposes several constraints on migration, including foraging time and the reduced metabolic scope available for migratory activity when energy is reallocated for foraging and digestion. As a consequence, most species rely heavily on energy reserves that they accumulate in the months preceding migration. In fact, in semelparous species such as Pacific salmon and lampreys, the alimentary canal and digestive organs undergo atrophy so that precious energy reserves are not wasted in maintaining these inactive tissues. In fishes that do not feed during migration, the energy available for migratory activity is finite; thus, energy management is a primary factor determining the success of a migrant.

The degree to which fishes deplete their energy reserves is highly variable both among species, and among different populations within a species. In some anadromous spawning migrations, energy depletion can be remarkably high,  $\sim 85\%$  of total energy stores. There is a correlation between the degree of energy depletion during migration and the prevalence of semelparity among fish populations - the more energy they deplete, the less likely they are to be repeat spawner. For example, there are no repeat spawners among American shad (Alosa sapidissima) migrating up the St. Johns River (Florida, USA), which deplete as much as 75-82% of their total stored energy reserves. However, American shad migrating up the more northern Connecticut River (New England, USA), which deplete only 35-60% of their stored energy, do repeat spawn. Nonetheless, while exhaustion of energy resources probably contributes to mortality in semelparous populations, it is not the only factor. This is evident by the fact that some semelparous populations migrate only a relatively short distance - not nearly far enough to exhaust their energy reserves, indicating that there are other genetic and/or environmental factors involved. Indeed, the mechanism of post-spawning death in semelparous species appears to involve a breakdown in glucocorticoid regulation, resulting in highly elevated levels of circulating corticosteroids and a consequent disruption of immune function. This may be part of a true but rapid senesence program.

Energy for migratory activity is stored as proteins, carbohydrates, and lipids. Lipids are the most energy dense form of energy storage, having an approximately twofold greater energy density  $(9.45 \text{ kcal g}^{-1})$  than both carbohydrates and proteins (4.1 and 4.8 kcal  $g^{-1}$ , respectively). Unlike higher vertebrates, which store lipids mainly in adipose tissue, fishes distribute lipid reserves among a variety of tissues, including adipose-like tissue in the viscera, muscle tissue, and the liver. Many fishes also possess a subcutaneous layer of fat. Studies of proximate tissue composition have demonstrated that both lipids and proteins are depleted during long-distance migrations. Carbohydrate levels tend to remain high, but this is because carbohydrates (glycogen and glucose) are used mainly to fuel short bursts of activity, and are then subsequently replenished through breakdown and conversion of lipids and/or protein.

The majority of energy mobilized during migration (excluding that used for gonadal development during spawning migrations) is used by the muscles for locomotor activity. In general, fishes have two types of muscles that are both anatomically and functionally distinct. Red muscle is organized into a thin longitudinal band beneath the lateral line and is ideally suited for powering slow and intermediate speed, high endurance swimming - the swimming that comprises most of a fish's routine activities. High-speed swimming is powered by white muscle, which comprises the bulk of the muscle mass, despite the fact that most fish species only occasionally invoke highspeed (aka burst) swimming. White muscle is fueled mainly by glycolytic (anaerobic) metabolism and is prone to fatigue (see also Swimming and Other Activities: Applied Aspects of Fish Swimming Performance). Moreover, during anaerobic swimming fish accumulate the metabolic by-product lactate, which can cause acidosis and even death. Reconversion of lactate to glycogen and rebalance of acid-base requires aerobic metabolism and can take as long as 24 h.

#### Environmental Factors That Influence Migration

Understanding how environmental variables influence migration is a popular theme in the study of migratory biology. The greatest challenge in studying how environmental factors influence migration is the fact that environmental variables are often highly correlated with one another, making it difficult to know which variables are the most relevant for influencing a migration. For example, in temperate climates there is a high degree of correlation between the length of day (photoperiod) and water temperature. Moreover, the relative importance of each environmental factor may be dependent on the local characteristics of the habitat in which the migration is occurring. Nonetheless, despite these challenges, a number of environmental factors have repeatedly been shown to influence migration in fishes.

Changing light levels are an important environmental stimulus for migratory activity. On a seasonal scale, changes in photoperiod provide calendar information that is used to initiate and synchronize the migratory activity of individuals within a population. Long-duration migrations such as the spawning migrations of Pacific salmon and Pacific lampreys (Lampetra tridentata) appear to be particularly dependent on photoperiod for synchronizing migratory activity. This probably reflects the fact that other environmental factors (e.g., temperature) that vary on a seasonal scale are more variable, and, therefore, less reliable. The daily (diel) alternation between night and day synchronizes migratory activity. Diel activity patterns fall into three categories - diurnal, nocturnal, and crepuscular. It is not clear for most fishes whether the diel pattern of migratory activity is a true endogenous circadian rhythm (see also Sensory Systems, Perception, and Learning: Circadian Rhythms in Fish) or a direct response to changing light levels. There is,

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however, evidence that fishes will adapt their diel activity to variations in light level. For example, nocturnal fishes often become active during the day when there is cloud cover, or when turbidity is high. Thus, the diel period in which a fish migrates appears to be related to its perceived risk of falling prey to visual predators.

Temperature can trigger and synchronize migratory activity in fishes. When temperature acts as a trigger, migration can be viewed as a form of behavioral thermoregulation (see also Behavioral Responses to the Environment: Temperature Preference: Behavioral Responses to Temperature in Fishes). This can occur under two conditions. First, in thermally heterogeneous environments, temperature may fluctuate beyond the range of thermal tolerance for a given population. Thus, the fish are forced to seek out a new thermal habitat. Second, the thermal requirements of the population may change. For example, the optimal temperature for growth may not be the same as for reproduction. In this example, temperature is the cause of the migration to spawning grounds. However, temperature is also a well-known synchronizing cue during spawning migrations. This is particularly true for migrations that are relatively short in duration. A good example of this is the springtime upstream migration of sea lampreys (P. marinus) in the Laurentian Great Lakes. Typically, the migration does not begin until temperatures in the streams exceed  $\sim 10$  °C. Thus, the migration begins later in cooler than average springs and earlier in warmer than average springs. This type of thermal threshold for migratory activity in spawning phase fishes is common and seems to have evolved in response to the strict thermal requirements of the developing embryos. A related temperature effect is slowed growth at low temperature, which causes more northern populations of Pacific salmon to rear in freshwater for another year before migrating to the ocean.

In fluvial habitats, discharge-related events can also have a marked influence on migratory behavior. The effect of discharge on migration can sometimes be difficult to interpret because changes in discharge are often associated with changes in other environmental factors, such as temperature and turbidity. Nonetheless, there is evidence that periodic increases in discharge, such as those that occur during the spring snow melt and after rain events, are commonly associated with peaks in downstream migratory activity (e.g., Atlantic salmon smolts, Salmo salar). Perhaps more surprisingly, increases in discharge are also commonly accompanied by peaks in upstream migratory activity (e.g., spawning migrations of white suckers, C. commersoni, and brown trout, Salmo trutta). In these instances, the benefits of higher water levels (e.g., greater protection from visual predators and easier access to headwater rearing sites) seem to outweigh the greater energetic costs of swimming against greater velocity. Moreover, it has been shown in adult Pacific salmon that some fish can utilize small-scale

reverse flow vortices to draft up-river with minimal swimming effort and thus can conserve high levels of energy during the migration. By contrast, in species with relatively poor swimming ability (e.g., American eels, *Anguilla rostrata*, and brook lampreys, *Lampetra planeri*), the cost-to-benefit ratio is apparently greater and increases in discharge may inhibit upstream migration.

There is fairly strong support for lunar phasing in some migrating fishes. In many cases, changes in migratory activity appear to be a direct response to variations in the intensity of moonlight. For example, upstream migratory activity in lampreys and eels is reportedly highest on nights with little moonlight. However, there is also evidence that some species may entrain to the lunar cycle. For instance, in masu (Oncorbynchus masou) and coho (Oncorbynchus kisutch) salmon smolts, circulating levels of the thyroid hormone thyroxin  $(T_4)$  peak during the new moon. This peak in T<sub>4</sub> is, in turn, a stimulus for downstream migratory activity. Lunar phasing has also been widely reported in diadromous species as they cross the seawater/freshwater boundary. However, in these cases, the relationship is generally believed to be indirect, and is likely a response to tidal variations, rather than changes in moonlight.

#### **Anthropogenic Impacts on Migration**

Human activities have a long history of interfering with fish migration. Probably, the most obvious way in which our activities disrupt migration is through the construction of dams and other structures (e.g., weirs and culverts) that act as barriers to migration in streams and rivers. Barriers disrupt stream continuity making it difficult, if not impossible, for fishes to reach upstream habitat (**Figure 3**). Even when a fishway is present at a barrier,



**Figure 3** Upstream-migrating rainbow trout (*O. mykiss*) attempting to surmount a lowhead dam located approximately 500 m upstream of Lake Ontario in Shelter Valley Creek (Grafton, ON, Canada). Photo courtesy of Thomas Binder.

it is typically selective in the species that it passes, and those fish that do navigate the fishway usually incur high costs, in terms of both time and energy (see also Hagfishes and Lamprey: Lampreys: Energetics and Development and Lampreys: Environmental Physiology). In addition, barriers can drastically alter the physical and chemical characteristics of a stream, and, thus, may reduce the abundance and quality of suitable stream habitat.

Toxicants and other chemical contaminants can also directly impact the migratory success of fishes. Contaminants may mask the odors that some fishes use to identify the home stream (see also Toxicology: The Effects of Toxicants on Olfaction in Fishes). Moreover, some toxicants cause physical damage to the sensory cells that mediate orientation. For instance, the olfactory and lateral line organs are particularly susceptible to heavy metals. Contaminants can also interfere with metabolism. Many toxicants have been shown to reduce swimming performance in fishes by limiting oxygen uptake and shuttling energy away from the swimming muscles. This increased metabolic load can also lead to premature mortality.

The final anthropogenic impact we will discuss is climate change. It is clear that the Earth is undergoing a relatively rapid change in its temperature regime and this will have an impact on migration success. First, higher temperatures, especially in temperate regions, are reducing the abundance of suitable habitat for many species, limiting the range over which migration can occur. Second, populations whose migrations are synchronized by photoperiod, rather than temperature, will experience higher temperatures throughout their migration. These higher temperatures will put greater metabolic demands on stored energy reserves and increase disease prevalence, resulting in a greater incidence of en-route migration mortality. Indeed, there is already evidence of this occurring in populations of Pacific salmon (see also Fish Migrations: Pacific Salmon Migration: Completing the Cycle). Third, higher temperatures could impact the reproductive success of spawning phase migrants. Embryonic and larval development is exquisitely sensitive to temperature. Even slight deviations from optimal temperatures can have drastic effects on development, including physical deformations and a reduction in the proportion of embryos that develop into juveniles. There is a paucity of information available on the long-term effects of small-increment increases in temperature on fishes, so it is difficult to predict to what extent individual species will be able to adapt their migration strategies to the new temperature regime. It appears, however, that species that undergo long-distance migrations may be most at risk (see also Temperature: Effects of Climate Change).

See also: Behavioral Responses to the Environment: Temperature Preference: Behavioral Responses to Temperature in Fishes. Fish Migrations: Eel Migrations; Pacific Salmon Migration: Completing the Cycle; Tracking Oceanic Fish. Hagfishes and Lamprey: Lampreys: Energetics and Development; Lampreys: Environmental Physiology. Hearing and Lateral Line: Lateral Line Neuroethology. Osmotic, Ionic and Nitrogenous-Waste Balance: Osmoregulation in Fishes: An Introduction. Sensory Systems, Perception, and Learning: Circadian Rhythms in Fish; Magnetic Sense in Fishes; Spatial Orientation: How do Fish Find their Way Around?. Swimming and Other Activities: Applied Aspects of Fish Swimming Performance. Temperature: Effects of Climate Change. Toxicology: The Effects of Toxicants on Olfaction in Fishes.

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