interval and float to the surface, where they transmit data to a low-orbit satellite system, such as Argos. Although the data transmission capability of such systems is limited at present, the accelerating use of electronic tags is likely to lead to rapid advances in descriptions of the behavior of migrating fish and also an increased understanding of how they find their way around the oceans. Good descriptions of the migration circuits of the commercially exploited species should help to improve assessment, management, and conservation.

Conclusions

Fish spawn so that their eggs and larvae are carried to good feeding grounds for their juvenile stages. The adults must subsequently compensate for this drift, if the population is to sustain itself. As they grow, fish become less dependent on the environment and some may migrate without any reference to ocean currents at all. Adults of some species, however, still use the current if there is an energetic advantage in 'hitching a ride,' especially in shallow tidal seas. How fish find their way around the oceans and whether they can truly navigate, or only obtain guidance from local clues, is not yet known. There is, however, physiological evidence that fish do have a magnetic compass sense and behavioral evidence to suggest the involvement of geophysical, and perhaps also topographical clues. Rapid advances in understanding are to be expected in the near future with the increasing use of sophisticated electronic tags that allow the tracks of migrating fish to be described in detail over seasonal timescales and long distances.

See also

Antarctic Circumpolar Current. Current Systems in the Atlantic Ocean. Demersal Fishes. Eels. Fish Larvae. Fish Locomotion. Fish Migration, Vertical. Fish Predation and Mortality. Fish Reproduction. Fish Schooling. Florida Current, Gulf Stream and Labrador Current. Kuroshio and Oyashio Currents. Pelagic Fishes. Salmonids. Tides.

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FISH MIGRATION, VERTICAL

J. D. Neilson, Department of Fisheries and Oceans, New Brunswick, Canada
R. I. Perry, Department of Fisheries and Oceans, British Columbia, Canada

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Introduction

While the often spectacular long-distance migrations of fish have been well described by the scientific community and are the source of considerable wonder to the general public, fish can also undertake migrations in the vertical dimension. Such migrations can occur at the earliest life history stages when fish are free-swimming, and can continue throughout their lives. Some species exhibit vertical migration behavior at certain stages of their life history, but not in others. In general, vertical migrations occur with 24-h periodicity and, to a lesser degree, display constancy in phase and amplitude. Attempts to explain the regularity of changes in depth distributions of fish have often involved the notion of circadian or endogenous rhythmicity. The term 'circadian' refers to a self-sustained rhythm of 24-h periodicity, either synchronized to a natural cyclic phenomenon or free-running. When migrations (or other events) occur with 24-h periodicity, they are said to be 'diel' in nature, in contrast to 'diurnal' and 'nocturnal', meaning day- and night-active, respectively.

Why study vertical migrations? From the ecological perspective, knowledge of vertical migrations advances our understanding of the interactions among fish, their predators and prey, and the abiotic environment. Vertical migrations are also mechanisms of energy transfer among the various depths of the ocean. Vertical migrations can also modify the horizontal distributions of fish by exposing populations to depth-specific variation in current strength. From the perspective of determining the number of fish in a population, ignoring vertical migrations can bias the interpretations of survey results. This is a particular problem for acoustic surveys that are unable to detect fish close to the bottom. If fish are periodically unable to be caught by the sampling gear, a potential bias may occur in the survey. Finally, from the perspective of a fishery, knowledge of vertical migration is critical in the choice and design of appropriate fishing gear and strategies.

Examples of Vertical Migration Patterns

Diel vertical migrations have been classified into two types. The first (type I, **Figure 1**) refers to the most common situation where fish move up in the water column at dusk, and down at dawn. As is the case in the example shown in **Figure 1**, some

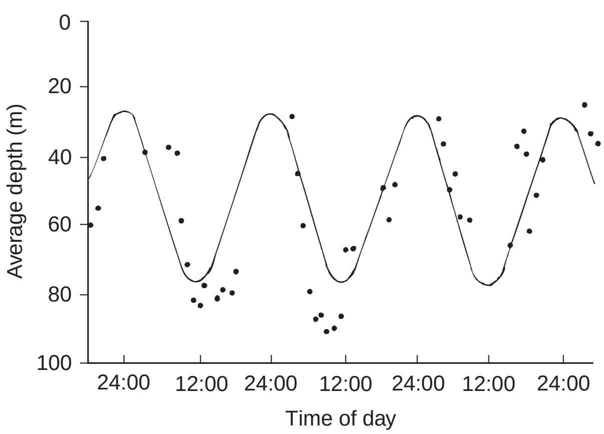

Figure 1 Vertical distribution of the sardine (*Sardina pilchardus*) in the Thracian Sea. The dots show the observed average depths, and the solid line shows the predicted average depth of the distribution according to a cosine function model based on the time of day. (Modified from Giannoulaki M, Machias A and Tsimenides N (1999) Ambient luminance and vertical migration of the sardine *Sardina pilchardus. Marine Ecology Progress Series* 178: 29–38.)

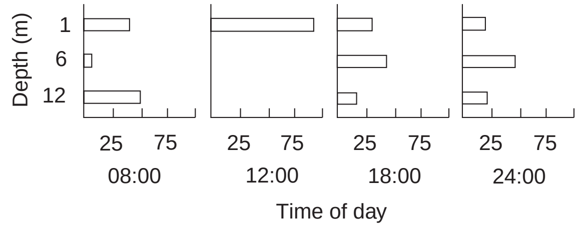

Figure 2 Vertical distribution of 15–21 mm gulf menhaden (*Brevoortia patronus*) larvae in the Gulf of Mexico expressed as percentages at four time intervals. (Modified from Sogard SM, Hoss DE and Govini JJ *et al.* (1987) Density and depth distribution of larval Gulf menhaden, Brevoortia patronus, Atlantic croaker, *Micropogonias undulatus,* and spot *Leiostomus xanthurus*, in the Northern Gulf of Mexico. *Fishery Bulletin.* 85: 601–609.)

authors model the distribution of the fish in the water column using sinusoidal functions.

Type II vertical migrations are the converse, with the fish being found higher in the water column during daylight hours (**Figure 2**) and closer to the bottom at night. Of the two, examples of type II vertical migration have been less frequently documented (see Neilson and Perry (1990) for a tabulation of literature reporting these types of vertical migration patterns).

Variation in Patterns of Vertical Migration

Any classification of vertical migration runs the risk of oversimplification. Variation in patterns of vertical migrations can occur among individuals, locations, species, and seasons. Some examples of the rich diversity in patterns of vertical migration are provided below.

Individual

Within a population, individuals that are larger than average often display a greater amplitude or range of depths during vertical migrations. In the case of Atlantic cod (*Gadus morhua*), for example, fish in their first year of life initially live in the pelagic zone. During this early stage, fish exhibit size-related vertical migrations, with larger individuals undertaking more extensive diel vertical migrations. Once these young fish reach a size of 80–100 mm, they become much more closely associated with the bottom. However, even when cod occur mostly on the bottom, they may still make vertical migrations whose amplitude appears positively related to their size. Many other species demonstrate this pattern of increasing range of vertical migration with increasing size, but few show the persistence across different life history stages illustrated by some Atlantic cod populations.

Population/Site

Variations in the pattern of vertical migration can occur because of differences in environmental conditions between locations. Site-specific variation in the pattern of vertical migrations occurs in populations of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with differences related to the availability of their prey. For juvenile haddock on both sides of the Atlantic, site-specific differences in patterns of vertical migration are observed. In the western Atlantic, differences in vertical migration patterns are again related to the relative abundance of prey. In many cases, it has been shown that the presence of thermoclines or pycnoclines can modify patterns of vertical migration. Meteorological conditions at a site may also influence vertical migration, particularly for those species such as redfish (*Sebastes* spp.) for which light is an important controlling factor.

Seasonal

Seasonal changes in patterns of vertical migration are shown by adult Atlantic cod in the Gulf of St. Lawrence. This population shows a type I vertical migration from mid-July to September. However, earlier in the year, a type II vertical migration is present. Similarly, larval herring in the Gulf of Finland occur in relatively deep water by day and closer to the surface at night during early summer, but the behavior is reversed later in the summer. The effects of increasing size and age are related to seasonal effects, and there are numerous studies demonstrating changes in patterns of vertical migration as fish develop.

Genus/Species

There is considerable intergeneric, interspecific, and even individual variation in patterns of vertical migration within a Pacific community of co-occurring species of myctophids (lanternfishes; **Figure 3**). In this example, most of the members of the myctophid community exhibit a constant type I vertical migration, with variation in the vertical extent of the migration. One species (referred to as a semimigrant) shows a facultative vertical migration, with part of the population remaining relatively deep in the water column regardless of the time of day. In this community, vertical migration appears to be a nighttime feeding strategy, with most species undertaking movement into the more productive upper portions of the water column. The semimigrants may be exhibiting an energy-conserving behavior, in which satiated fish remain in the relatively

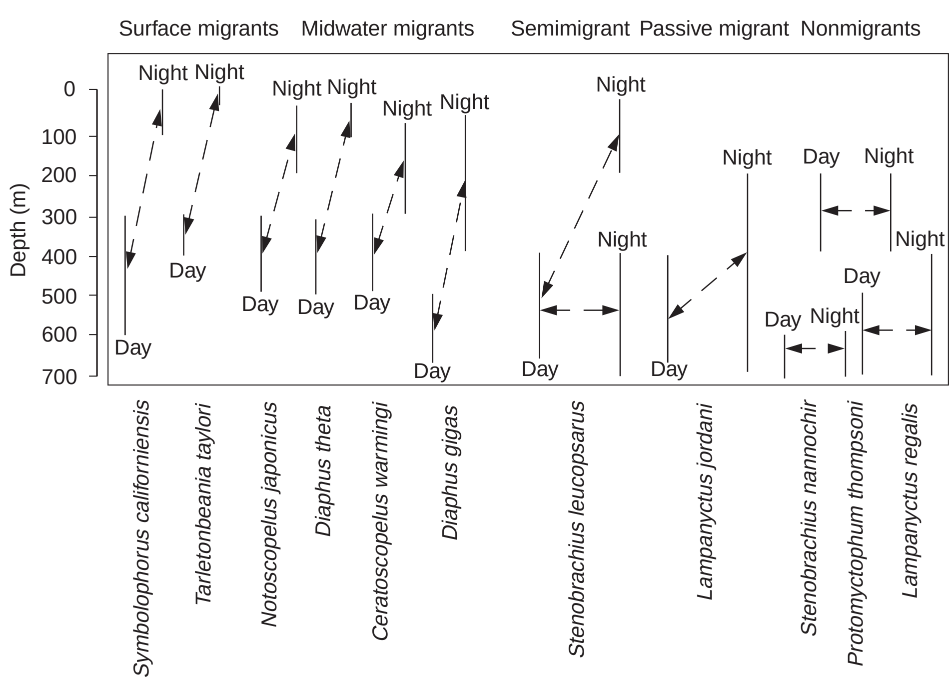

Figure 3 Changes in the day–night vertical distribution of a community of myctophids (lanternfishes) in the western North Pacific. (Modified after Watanabe H, Moku M, Kawaguchi *et al.* (1999) Diel vertical migration of myctophid fishes (Family Myctophidze) in the transitional waters of the western North Pacific. *Fisheries Oceanography* 8: 115–127.)

cool (deeper) water at night. This behavior is a further example of variation in patterns of vertical migration at the individual level.

Potential Factors Influencing Vertical Migrations of Fish

From the examples discussed above, it is clear that variations in amplitude of vertical migrations occur frequently. Variations in phase and period are much less common, however, leading some workers to suggest that vertical migrations are an example of an endogenous circadian rhythm that is entrained by some cyclic natural cue. Natural processes that have been proposed to influence the patterns of vertical migration include light, tide, food, and other species.

Light

For animals in the photic zone of the world's oceans, the daily cycle of light and dark is perhaps the most powerful environmental signal available. One of the earliest reports indicating light as a primary factor in vertical migration was by Russell in 1927, who suggested that zooplankton occupied depths that had an optimum light intensity. He further suggested that, as animals moved away from this optimum intensity, physiological reactions controlled by photochemical mechanisms stimulated them to return to the zone of optimum light intensity. Later reviewers concluded there was abundant (albeit circumstantial) evidence implicating light as a significant factor regulating the vertical migration of fish. This evidence included the timing of vertical migration with respect to dusk and dawn, a lack of vertical migration at high latitudes, and the results from experiments with artificial lights and during solar eclipses.

Researchers have elaborated on the concept of a preferred level of illumination by developing mathematical models to describe the diel vertical migration of fish based on light, and have developed expressions to predict the depth range over which vertical migration should occur. However, other studies have suggested that differences in water transparency will have a stronger influence on diel vertical migrations of fish than the surface illumination, since the attenuation coefficient determines the light intensity at depth.

The interpretation of these studies is that light has an important role in mediating vertical migrations of fish. Compared among species, however, light may be more important for some fish such as the herrings and sardines, but it is not the sole determinant of vertical migration.

Tides

For animals that live in near-shore and continental shelf regions, the daily variation of the tide is another powerful rhythmic environmental signal that could influence the behavior of fish. Several species of intertidal fish show strong rhythms of locomotor activity at near-tidal periods. For example, fish living on sandy shores (e.g., the sand goby *Pomatoschistus minutus*) are more active in the laboratory at times corresponding to ebb tide in their natural environment, which may prevent them from becoming stranded as the tide recedes. In contrast, fish on rocky shores (e.g., Blenniidae) become more active in the laboratory at times corresponding to high tide in their natural environment, which may relate to their habitat being tide pools and the fact that high tide provides an opportunity for them to move about more widely.

The larvae of some estuarine fish have developed behaviors that appear to enhance their retention within the estuary, or enhance their movement from offshore spawning grounds into estuarine nursery areas. For example, hogchoakers (*Trinectes maculatus*) in a Maryland estuary show a persistent rhythmic activity with maximum activity corresponding to slack tide, even under conditions of continuous light, which may help them maintain their position. The larvae of other species of estuarine fish have been observed to remain on or near the bottom during the day and during ebb tides, but to move off the bottom at night and during flood tides, which would tend to transport them towards shore or into the estuary.

Mechanisms that have been suggested to enable fish to detect tidal currents include physical factors such as changes in light, turbidity, turbulence, temperature, and salinity. Many of these have been criticized as tidal cues, however, because they will also vary as a result of nontidal factors such as clouds and storms. Other suggested factors include olfactory cues indicating currents toward or away from the coast, direct detection of flow direction or reversal, and induction of electric fields in the water.

Food

Another obvious possible driver of vertical migration in fish is the vertical migration of their prey, which includes both zooplankton and other fish. The presence or absence of prey can restrict or promote vertical migrations of fish, in particular of their early stages. For example, downward migrations of young walleye pollock (*Theragra chalcogramma*) in the Bering Sea are delayed when food abundances are high, but enhanced when food is low in the upper waters. Other species of fish, e.g., capelin (*Mallotus* sp.), Atlantic herring (*Clupea harengus*), and mesopelagic species, have been observed to follow closely the vertical distributions of their zooplankton prey. Adult cod follow a type I vertical migration pattern when feeding on pelagic zooplankton, but switch to a type II vertical migration pattern when feeding on benthic animals. When it occurs, the less common type II pattern appears to be related to the movements of the preferred prey.

Commensal Species

In open pelagic waters, the young stages of certain species of fish are often found closely associated with gelatinous zooplankton (e.g., jellyfishes). Some of these jellyfish undertake vertical migrations, and so the fish associated with them follow along. In a plankton sample this may appear as independent vertical migration by these fish, unless the sample is carefully observed for gelatinous zooplankton (or their remains).

Theories to Explain Diel Vertical Migration Behavior

A number of theories have been proposed to explain the occurrence and persistence of vertical migration across a broad range of species.

Bioenergetics

Considering the widespread occurrence but highly variable patterns of vertical migratory behaviors in fish, the question arises as to what advantages they might provide. For a behavior to persist and become widely distributed among different species, it must confer an evolutionary advantage that increases the survival (fitness) of an individual. One way that fitness is enhanced is by increasing individual growth rates. This implies that fish should feed where prey are most abundant and are readily available to the fish. In 1993, Bevelhimer and Adams, building upon work by Brett in 1971, noted that the most advantageous locations for feeding (and subsequent growth) are not necessarily those with the greatest food density. Other factors that are significant include the potential feeding rate, stomach capacity, and temperature effects on stomach evacuation rate, respiration rate, and other metabolic processes. These observations lead to the bioenergetic advantage hypothesis for vertical migration of fish, which states that fish should feed where the net intake of energy is maximized, then spend their nonfeeding time where energetic costs (e.g., respiration) are minimized, providing that the energetic costs of migrating between these two locations are minimal.

In most marine systems and when prey are not limiting, this bioenergetic hypothesis implies that vertical migrations will occur between deeper, cooler waters with less prey and shallower, warmer waters with more prey – a type I pattern. It can also explain the type II migration pattern if the fish are acclimated to warmer temperatures but make foraging excursions into colder water, where prey may be more abundant in some situations. But what happens when the vertical thermal gradient breaks down, either temporarily owing to storms and a deeper mixed layer, or to seasonal changes in stratification? For some fish at least, such as juvenile salmon in lakes, their vertical migratory behavior appears to stop.

If food is not abundant, the vertical migration patterns predicted by the bioenergetic hypothesis can be changed. Studies show that juvenile walleye pollock remain in warmer upper layers when food is easily available, but migrate into deeper, colder waters when prey densities are reduced. Further experimental studies show that juvenile walleye pollock switch to an energy-conserving behavior when food is limiting, by moving increasingly into colder water so that the optimal temperature for growth also decreases. Therefore, prey abundance and its availability to a fish species can be an important modifier of diel vertical migrations by that fish species.

Predation

The potential for the death of fish due to predation is another strong modifier of the vertical distribution of fish. Japanese sand eels (*Ammodytes* spp.) and northern anchovy larvae (*Engraulis mordax*) exhibit a type II vertical migration pattern in which they cease swimming at night and sink. This inactivity may reduce attacks by predators that detect prey through motion and vibrations. In 1978, Eggers suggested a predator avoidance hypothesis to explain the vertical migratory behavior of juvenile sockeye salmon. Although these studies were conducted on fish in fresh water, salmon are often used as models for pelagic marine predators because they are relatively easy to study. In this hypothesis, fish become distributed at depths where the searching ability of visual predators is reduced (i.e., at the minimum irradiance level that maximizes the reaction distance of a predator to its prey). This was subsequently combined with the bioenergetic hypothesis to suggest that the characteristic patterns of diel vertical migration are a three-way trade-off

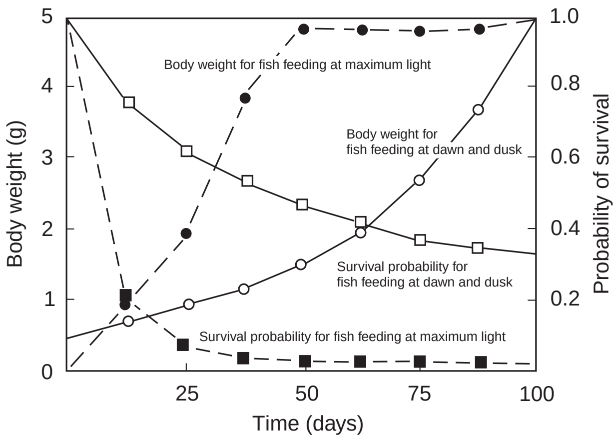

Figure 4 Results from a computer simulation model of two feeding behaviors by a planktivorous fish. Dashed lines represent the growth (●) and survival (■) of a fish feeding during the maximum light intensity, whereas the solid lines represent growth (○) and survival (□) for a fish feeding at dawn and dusk and migrating below the upper water layer during the day. Although growth is slower, survival is clearly enhanced for the fish that feed at dawn and dusk-feeding. (Modified after Clark CW and Levy DA (1988). Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *American Naturalist* 131: 271–290.)

(optimization) between predator avoidance (minimizing predation mortality), maximizing food intake, and minimizing metabolic losses. In 1988, Clark and Levy developed a model of this trade-off, based on juvenile sockeye salmon and their visual predators. The model predicts that the ratio of risk-of-mortality to feeding rate for juvenile sockeye should be minimized at the low and intermediate light levels that occur at dawn and dusk, which they termed the 'antipredation window'. The optimal behavior for survival, therefore, would be for the pelagic planktivorous fish to migrate into surface waters to feed during dawn and dusk and to migrate to cooler less-illuminated deeper waters during the day (**Figure 4**).

Optimization Models

Rosland and Giske have developed a similar optimization model to describe the vertical behaviors of the mesopelagic planktivore *Maurolicus muelleri*, a common species in the fiords and continental shelf of Norway. In winter, the juveniles of this species

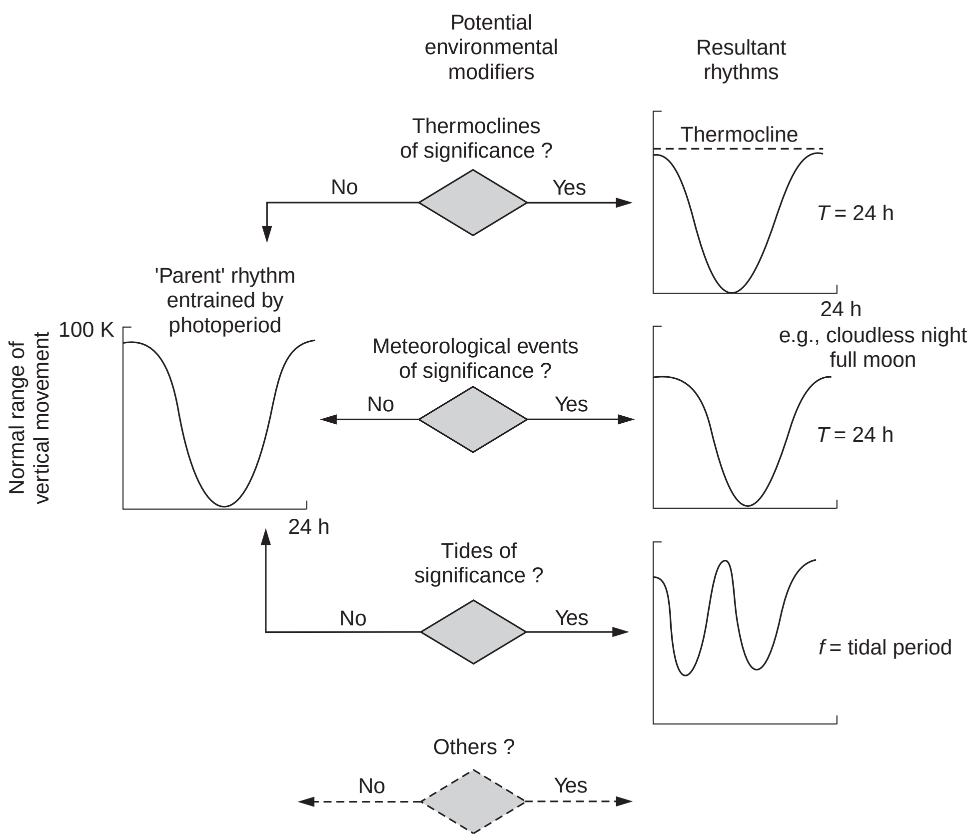

Figure 5 Diagrammatic figure showing how some environmental features could modify a cyclic vertical migration that is otherwise entrained by photoperiod. (After Neilson JD and Perry RI (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? *Advances in Marine Biology* 26: 115–168.)

migrate over the upper 100 m, rising to the surface at dawn and dusk. The adults, in contrast, remain below 100 m, with no distinct vertical migration pattern until summer, when they migrate to the surface at dawn and dusk. The optimal depth position was calculated in their model as a balance between feeding opportunity and risk of mortality from predation, which correctly predicted the dawn and dusk migration and feeding pattern. The observed differences in vertical migratory behaviors of this species, as an example, depend on individual differences in age, size, energetic state, variations in the seasonal environment, and an optimization between minimizing predation losses, maximizing food intake, and minimizing metabolic losses that may depend on different life history requirements.

Conclusions

Diel vertical migrations of marine fish are relatively common phenomena that occur in many species and at different life history stages. The relative constancy of their diel periods is consistent with the notion of an underlying circadian rhythmicity. The process of vertical migration also appears to be a facultative one in many cases, as the pattern of vertical migration can be changed by a number of factors. An example of a hypothetical system of multiple controls on diel vertical migrations is shown in **Figure 5**. In this model, an endogenous rhythm of vertical migration is determined initially by photoperiod. Under certain circumstances, the vertical migration pattern of the fish switches from being entrained by a light–dark cycle to entrainment by the tidal cycle, for example, with the result that the period of vertical migration activity is modified. Likewise, events such as a full moon on a cloudless night might act to modify the rhythm by suppressing the amplitude of the vertical migration.

Such variations in vertical migration pose profound difficulties for surveys of the abundance of fish. To reduce these problems, researchers may study different life history stages or use different sampling techniques that include the range of vertical migration, when this is known.

See also

Demersal Fishes. Fish Feeding and Foraging. Fish Larvae. Fish Locomotion. Fish Migration, Horizontal. Intertidal Fishes.

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FISH PREDATION AND MORTALITY

K. M. Bailey and J. T. Duffy-Anderson, Alaska Fisheries Science Center, Seattle, WA, USA

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Overview

Not only do fish prey on one another, but almost every other type of animal in the sea from jellyfish to whales and seabirds eat enormous quantities of fish. Apart from some less usual conditions (such as outbreaks of disease, mass starvations, harmful algal blooms, or extreme over-fishing) predation by other animals is the largest source of mortality of fishes in the sea. Among the most voracious of these predator groups, other fishes consume the lion's share, but in some seas marine mammals also consume large amounts (**Figure 1**). Predation mortality is generally highest on juvenile fishes, but fishing mortality