Energetics of Foraging Decisions and Prey Handling

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Glossary

Aerobic scope The capacity for an animal to increase its level of aerobic metabolism beyond that which is required for maintenance alone; it sets the capacity for oxygen-consuming physiological processes that an animal may perform at a given time. Aerobic scope is the difference between minimal and maximal oxygen consumption rate.

Fitness (Darwinian) Describes the ability of a genotype to reproduce and propagate into the next generation. It is influenced by the survival and fecundity (reproductive output) of individuals.

Foraging Behaviors performed by animals when searching for, identifying, capturing, subduing, and consuming food.

Ideal free distribution A theoretical concept used to describe how animals distribute themselves across food patches; This distribution predicts that animals will disperse across patches in a manner that is proportional to the food available in each patch.

Maximal metabolic rate The maximum metabolic rate achieved by an animal. If measured as O_2 uptake, it would be termed V_{O2max}.

Optimal foraging theory A theoretical framework used to study the foraging decisions of animals. Incorporating several assumptions, it predicts that animals should forage in a manner that maximizes the net energetic intake.

Piscivore An animal that feeds on fish, either exclusively or as part of a wider dietary range.

Planktivore An animal that feeds on plankton, either exclusively or as part of a wider dietary range.

Prey handling Behaviors performed by a predator during the capture and consumption of a prey item, including the subduing, orientation, or sectioning of prey (biting, tearing) before consumption.

Standard metabolism In ectotherms, this term describes the minimal level of aerobic metabolism (per unit time) required for maintenance functions to sustain life. In this sense, it is analogous to basal metabolism in endotherms, though standard metabolic rate (SMR) is strongly influenced by environmental temperature and so it is not always constant within an individual.

Introduction

Fish must consume enough food to satisfy their energetic requirements for maintenance, growth, activity, and reproduction. From an evolutionary perspective, natural selection should favor the most efficient foragers. This concept forms the basis of optimal foraging theory (OFT), which posits that animals should behave in a manner that maximizes the rate of net energy intake. Energy input in the form of food is required to sustain biological function, and so it is assumed that net energetic intake is positively correlated with fitness. To achieve a maximum rate of energy accumulation, a fish must not only optimize energy intake through food ingestion, but also minimize the amount of energy spent on foraging. Another important consideration is time; time spent on capturing or handling prey may detract from further foraging (i.e., energy acquisition), or other important behaviors such as predator avoidance or reproduction.

While OFT provides a useful foundation for predicting how fish should behave while foraging, in reality, fish are subject to constraints that may lead to suboptimal energetic behavior. When observations do not agree with the theoretical predictions of OFT, however, it is often interesting and informative to study why this is so. There are numerous factors (e.g., predator avoidance) that affect fitness besides net energy accumulation, and it is impossible to simultaneously optimize all of these components in the performance of a behavior or physiological process. Furthermore, because all biological functions
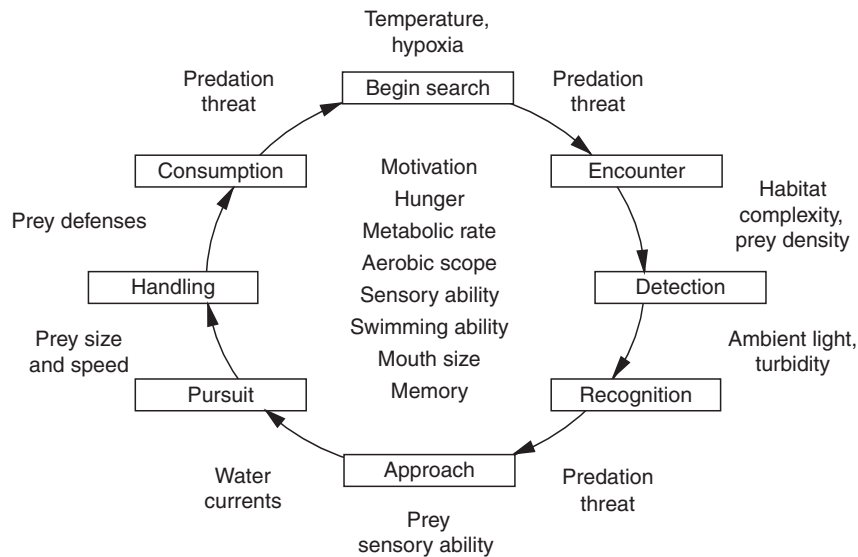
Figure 1 Components of a typical foraging cycle in fish, beginning with the onset of searching for prey and ending with prey consumption. Inside the circle are various internal factors (e.g., physiological and morphological characteristics) that may influence the outcome of the various phases of the foraging cycle. Outside the circle are various external factors (e.g., environmental variables and prey characteristics) that may influence the energy expenditure by the predator that occurs during each phase, the likelihood of each phase occurring, or the outcome. External factors most relevant to foraging energetics are listed alongside points in the cycle where they may have the greatest effect. Note that predation threat may have effects at numerous points along the foraging cycle. This is because a predatory threat could cause a foraging fish to abandon foraging behavior at all points throughout this cycle. Adapted from Hart PBJ (1997) Foraging tactics. In: Godin J-GJ (ed.) *Behavioural Ecology of Teleost Fishes*, pp. 104–133. New York: Oxford University Press, by permission of Oxford University Press.

require finite resources of time and energy, there are often inescapable constraints on their execution that restrict fish from maximizing their net-energy gain. While individual fish may not always forage in a manner that is energetically optimal, they still should adjust their behavior and physiological function within these trade-offs to maximize their overall fitness (**see also Food Acquisition and Digestion**: Dietary Requirements of Fish Under Culture Conditions).

After a fish is motivated to begin feeding, a typical foraging sequence proceeds with a search phase, followed by prey detection and recognition, an approach by the predator and a possible pursuit and attack, some handling of the prey, and then finally, consumption of the prey item by the predator (**Figure 1**).

There are numerous energetic trade-offs and constraints that affect the foraging decisions of fish at all points throughout this sequence.

The Motivation to Feed – When to Forage?

Internal Factors

Hunger

Individuals provided with an unlimited supply of food after fasting will initially display a high feeding rate, presumably due to increased hunger, but this rate will decrease as the animal satiates. Circulating concentrations of certain metabolic substrates and endocrine and paracrine substances are also important in regulating appetite (**see also Integrated Function and Control of the Gut**: Endocrine Systems of the Gut and **Gut Anatomy and Morphology**: Gut Anatomy). For example, injection of glucose, amino acids, or leptin tends to decrease feeding rates, whereas circulating ghrehlin will increase feeding. The change in appetite caused by fluctuations in metabolic substrates is mediated through hormonal and paracrine signaling between the gut and the brain and within the brain itself. Appetite can also be stimulated by certain olfactory and gustatory cues from the environment such as waterborne amino acids and carbohydrates.

Metabolic rate and aerobic scope

It is often hypothesized that the energetic requirements of maintenance may directly influence the motivation to forage in individual fish, possibly by increasing the frequency or intensity of hunger bouts. In ectotherms, the minimum amount of energy required to perform life-sustaining physiological functions can be quantified by measuring standard metabolic rate (SMR) (**see also Energetics**: General Energy Metabolism). While a relationship between resting metabolic demand and foraging motivation is often assumed to exist, there have been few attempts to confirm this link experimentally. Feeding

rates tend to increase with temperature in fish, and this is at least partially due to an associated increase in metabolism and energetic demand. Still, the effect of metabolic rate on appetite in individual fish, independent of temperature, is not well understood. Indeed, territorial species may even show a negative correlation between SMR and foraging activity; aggressive individuals with correspondingly high SMRs may initially devote more time and energy to territorial defense as opposed to foraging. In the long term, however, this strategy may lead to increased foraging opportunities once a high-quality territory is established.

Another metabolic trait that may have an important influence on appetite is aerobic scope. Aerobic scope represents the capacity of an animal to increase its level of aerobic metabolism above that which is required for maintenance, and is bounded at its upper limit by an animal's maximal aerobic metabolic rate (MMR; **see also Swimming and Other Activities**: Energetics of Fish Swimming and **Ventilation and Animal Respiration**: The Effect of Exercise on Respiration). This aerobic scope sets a limit on the simultaneous performance of oxygen-consuming physiological processes within an animal. In many fishes, feeding rate correlates well with aerobic scope, presumably because an elevated aerobic scope can accommodate the increase in metabolic rate associated with digestion and nutrient assimilation without compromising other physiological functions. Further research is needed to examine the relationship between appetite, maintenance metabolism, and aerobic scope in fish.

External Factors

Predation threat

Foraging makes animals more obvious to predators and also reduces the vigilance of individuals toward potential threats. For these reasons, fish generally decrease foraging in the presence of a predatory threat, and predator avoidance is a major constraint on the ability to maximize energy intake through foraging. In general, laboratory fish offered food in the absence of a predator eat more and grow faster than when a predator is present. The exact magnitude of such foraging reductions is influenced by the physiological state of an individual. Hungry or food-deprived fish display increased feeding in the presence of a predatory threat relative to that in well-fed fish, and they will resume feeding sooner after fleeing from an attack. It also has been shown that individual fish have distinct personalities, consistently behaving either more or less risky under the threat of predation (**see also Social and Reproductive Behaviors**: Dominance Behaviors). There is evidence to suggest that these behavioral differences among individuals are linked to genotype and intrinsic physiological factors such as metabolic rate,

with individuals with increased SMR displaying increased risk-taking behavior during foraging. For example, in juvenile Atlantic salmon (*Salmo salar*), individuals with increased SMR tend to forage outside of covered areas more often and are thus able to attain higher rates of feeding. In contrast, larvae of many fish species decrease foraging under the threat of predation despite their high mass-specific metabolic rate, thereby suffering possible decreased growth, depletion of lipid stores, and increased mortality. However, growth-enhanced transgenic fish have such high appetites that they take more risks to feed, and as a result, are often eaten by predators in experimental situations (**see also Cellular, Molecular, Genomics, and Biomedical Approaches**: Growth Hormone Overexpression in Transgenic Fish).

Temperature

Feeding in fish increases with increasing temperature until a peak at some intermediate species-specific temperature, and then shows a strong decline with further temperature increases, creating an optimum temperature for feeding and hence growth. The initial increase in feeding with temperature parallels the temperature-driven rise in metabolic rate. Interestingly, metabolic rate generally continues to increase with temperature beyond the point at which feeding rate begins to decline, and so changes in metabolic demand cannot solely be responsible for temperature-related changes in foraging motivation at least at these higher temperatures. Aerobic scope in fish follows a parallel pattern of response to temperature change as does feeding rate. In many species, the temperature at which aerobic scope is highest is also the peak temperature for feeding and growth rates (**see also Food Acquisition and Digestion**: Cost of Digestion and Assimilation, **Swimming and Other Activities**: Cellular Energy Utilization: Environmental Influences on Metabolism, **Temperature**: Membranes and Temperature: Homeoviscous Adaptation).

Hypoxia

Decreased environmental oxygen (hypoxia) strongly decreases appetite in water-breathing fish. Indeed, many fishes completely halt feeding when environmental oxygen becomes limiting. This is most likely due to the tremendous decrease in aerobic scope that occurs during hypoxia (both SMR and MMR decrease during hypoxia, but MMR shows a much greater decline), and likely serves to conserve some of the limited aerobic scope for other physiological processes besides digestion (**see also Integrated Response of the Circulatory System**: Integrated Responses of the Circulatory System to Hypoxia and **Hypoxia**: Metabolic Rate Suppression as a Mechanism for Surviving Hypoxia). Despite these constraints, some fish species that live in stratified waters (e.g., anchovy *Anchoa* spp.; mudminnow *Umbra limi*) have

been observed to enter hypoxic-water layers briefly to capture prey, though they return to normoxic waters for digestion.

Habitat Selection – Where to Forage?

Food Availability and Predation Risk

As mentioned, fish that reduce foraging activity in the presence of an immediate predatory threat will incur an energetic cost, but such encounters can be avoided altogether if fish occupy a safer habitat. Often, this results in a behavioral trade-off between occupying a dangerous, resource-rich habitat, or a safe, resource-poor habitat. For instance, young lake fishes have increased foraging success while feeding on zooplankton and other prey in open environments. These same habitats, however, leave young fish exposed to being preyed upon, and so they instead may choose to forage in less-profitable but highly structured habitats that provide shelter. Such habitat shifts occur in environments with high predator populations and can cause reduced growth rates in young fish.

The relationship between predator-mediated habitat selection and energetic or nutritional demand in fish has not been investigated directly, though food-deprived fish tend to occupy habitats that are dangerous and more profitable as well. It is possible to estimate the energetic equivalence of predation risk in a dangerous foraging patch by observing predator-induced deviations from the ideal free distribution. Fish foraging on food items that are homogeneously distributed across two foraging patches show a nonequal distribution between the patches when one patch contains a predator. Fewer individuals use the risky patch, but those that do have greater access to food (per fish). The difference in food intake (per fish) between individuals in the risky and safe patches can be considered as the energetic equivalent of the imposed risk. This approach has been useful for gaining insight into the effects of factors such as gender and morphology on habitat selection, and could also be used to investigate the physiological thresholds that cause fish to select dangerous but profitable habitats (e.g., the effect of SMR, RMR, or aerobic scope on habitat selection).

Flow Velocity

For stream-dwelling fishes (e.g., juvenile salmonids), the choice of foraging location is influenced by localized differences in water flow. The encounter rate with drifting prey increases with flow velocity, but the actual number of prey captured declines at relatively high flows because prey are more difficult to catch. The energetic cost of foraging also increases with increasing flow velocity, because fish need to swim faster to keep up with the prevailing current. Furthermore, the energy spent on unsteady swimming during pursuits and prey capture increases with flow velocity due to increased drag. As a result of these opposing costs and benefits, there is an optimal velocity at which the net energy gain will be maximized. Observations in the laboratory and the field have shown that the flow velocity chosen by fish often matches with the predicted optimal velocity, though the exact foraging location selected also depends on factors such as prey size, prey density, the level of predation threat, and competition with other fish.

Territoriality and Aggression

Territoriality for foraging patches is well known in reef fish and stream-dwelling salmonids, though the energetic aspects of territoriality have been primarily studied in the latter (see also Social and Reproductive Behaviors: Dominance Behaviors). In juvenile salmonids, more aggressive individuals defend feeding territories by chasing away intruding conspecifics. The energy spent on these behaviors, per unit time, is at least twice the amount used for maintaining position in a flowing stream alone. Still, territorial fish have higher rates of feeding and growth compared to those that are not able to hold territories. Once a territory is established, the resident fish apparently spends less time and energy on aggressive behaviors, while nonterritorial fish continue to engage in aggressive encounters with other fish. Territorial fish also spend less energy on swimming because they spend more time maintaining station as opposed to maneuvering at an angle through currents.

Despite these apparent benefits of territoriality, the profitability of aggressiveness is context dependent. When aggressive and nonaggressive fish are given equal access to food, it is the nonaggressive individuals that grow faster. This may be due to the more-aggressive fish generally spending more energy on activity or having a higher SMR. Therefore, while aggressiveness may be beneficial when food resources are limiting, increased aggression apparently costs in situations where it is not possible to monopolize food resources.

Searching for Food – How to Forage?

Search Speed

Some fish species (e.g., tuna and salmonids) cruise through their environment actively searching for prey, whereas others remain nearly stationary, lying in wait until they ambush unsuspecting prey that happen to pass (sit-and-wait foragers; e.g., pike *Esox* spp.; sculpin *Myoxocephalus* spp.).
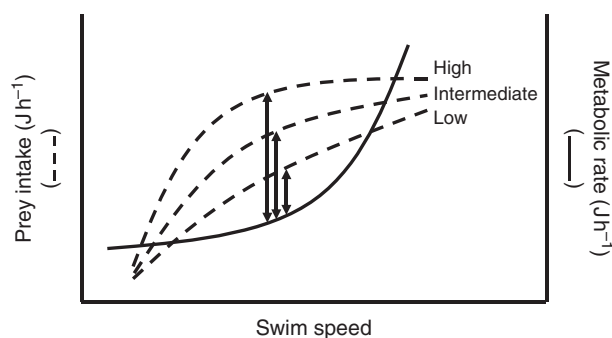
Each of these strategies carries distinct costs and benefits: cruise foragers incur greater locomotory costs, but

increased prey-encounter rates; ambush foraging is less costly, but prey encounters are relatively rare. Between these two extremes, there is a continuum of search strategies, in which individuals swim through their environment but frequently pause to scan for prey (saltatory foragers; e.g., bluegill *Lepomis macrochirus;* arctic grayling *Thymallus arcticus;* and white crappie *Pomoxis annularis*). Species that use this strategy may be closer to either the cruise or sit-and-wait foraging strategies along the continuum depending on the relative durations of the swimming and pausing phases. This pattern of intermittent movement may allow for better detection of prey during pauses, and heighten the ability to detect predators while foraging. A potential drawback of saltatory foraging is that locomotory costs may be increased due to frequent acceleration and deceleration. On the other hand, saltatory searching may ensure that a given volume of water is searched more thoroughly, and so less swimming will be needed to search a given space.

For planktivorous fishes, including the larvae of many species, rates of prey intake increase with swimming speed, gradually level off, and possibly even decrease at high speeds (**Figure 2**).

At the same time, the costs of locomotion (energy per unit time) increase curvilinearly with swimming speed. Based on these considerations, fish should forage at the speed that provides the greatest difference between energy cost and energy return. Factors such as habitat and prey density also play a role in determining the optimal-foraging speed; fish should (and usually do) swim faster at low prey densities and slower at high prey densities. Fish also swim faster while foraging when they are hungry as compared to when they are well-fed.

Laboratory and field observations generally match these theoretical predictions, though in some situations they do not. For example, fish foraging at high densities (e.g., fish shoals) tend to swim faster than their theoretically optimal speed. This could be due to the increased density of conspecifics and competition for available food, or differences in hydrodynamic efficiency when swimming in large groups. In other instances (e.g., some flatfish species), fish may not be able to achieve their optimal swim speed due to limited maximal aerobic capabilities. Furthermore, in some species (e.g., juvenile lumpfish *Cyclopterus lumpus*), foraging at the optimal swimming speed may comprise such a significant portion of the available aerobic scope that it would constrain the ability to perform additional physiological functions.

Search Path

Another consideration when actively foraging is the path that will be taken while scanning for prey. In habitats with low prey concentrations or prey that are clumped in small or spatially discrete patches, fish tend to search in a directed manner with low turning rates and low overlap of areas that have been searched already. In this type of directed foraging, the amount of spatial overlap with previously searched areas also decreases with experience and familiarity with a search range, which serves to decrease the energetic costs of searching. By contrast, fish feeding in habitats with high prey concentrations search in a more convoluted path with a higher turning rate and increased spatial overlap. A high turning rate while searching translates to increased foraging costs, but the fish are able to search a patch more thoroughly for prey.

The ability to search a given volume of water is not constant throughout ontogeny. Due to their limited visual range and swimming ability, larval fish have a very restricted search space as they move through the water column. The larvae of a few species have acquired interesting morphological adaptations to improve search efficiency, such as protruding eye stalks that increase visual range and therefore decrease the amount of swimming that is required to search a certain volume. As fish increase in size, their sensory systems and swimming ability improve, allowing them to search larger volumes of water more efficiently.

Figure 2 Schematic diagram illustrating changes in prey intake and metabolic rate (as estimated by measuring oxygen uptake) with swimming speed at three different prey densities (high, intermediate, and low). The predicted optimal swim speed at each density is that which allows for the greatest net energetic intake (largest difference between potential energy consumption and the costs of locomotion while foraging). Based on data from Ware DM (1975) Growth, metabolism and optimal swimming speed of pelagic fish. *Journal of the Fisheries Research Board of Canada* 32: 33–41 and Dabrowski K, Takashima F, and Law K (1988) Bioenergetic model of planktivorous fish feeding, growth and metabolism: Theoretical optimum swimming speed of fish larvae. *Journal of Fish Biology* 32: 443–458.

Foraging Modes

Many species display behavioral flexibility while searching for prey and are able to switch between alternate foraging modes in response to varying

environmental conditions. Some species, for example, cruise forage when prey densities are low (e.g., lumpfish, juvenile salmonids, and nase *Chondrostoma nasus*), but become ambush foragers at high prey densities. Among ectothermic species that display search mode-switching behavior, the more energetically costly search mode is generally used when prey is scarce or in dispersed patches, and the less costly mode is used when prey is abundant or aggregated. This pattern is directly opposite to that observed in endotherms, for which the more costly search mode is used at high prey densities. This difference is most likely due to differences in metabolic demand; the relatively high metabolism of endotherms means that active foraging is only economical when prey is abundant. Meanwhile, less energy is required for activity in ectotherms, permitting them to actively seek out food when prey is scarce and conserve energy when prey is abundant. Reducing activity in this manner is also an effective way to conserve space within their aerobic scope, which is already relatively limited as compared to that of endotherms.

Prey Selection – What to Forage?

Prey Type and Size

The basic prey model (BPM), an offshoot of OFT, states that when selecting prey, energy gain should be maximized per unit of prey-handling time. Prey-handling time is often defined as the time between prey capture and ingestion, but many researchers also include the time used to pursue prey after detection. For a given prey type (e.g., mussels and minnows), large prey contain more energy than small prey but will take longer to capture, subdue, and consume. In fact, for a given prey type, there is usually an exponential increase in both the time and energetic costs of handling with size. Therefore, a trade-off exits between the energy provided by larger prey, and the time and energy required for their capture and handling. Studies with planktivorous fishes have found general agreement with the BPM, because these species tend to minimize time and energy spent foraging by selecting the largest prey items available. For piscivorous fishes, however, prey are often smaller than predicted. This is likely related to the inherent difficulty in capturing larger prey fishes, and variability regarding the energetic cost during pursuits. Piscivores may preferentially attack smaller fish because of the reduced chances of an escape or unexpectedly costly pursuit. Alternatively, it has been suggested that piscivores are indeed not size selective, but that estimates of prey-size preference based on gut contents simply reflect differential size-based capture success. There are also numerous anecdotal accounts of individual fish attempting to swallow prey items much larger than normally would be expected. For instance, it is not uncommon to observe a shorthorn sculpin *Myoxocephalus scorpius*, an ambush predator, with the tail of a much larger fish protruding from its mouth.

Numerous additional factors may affect moment-to-moment decisions when selecting prey. Habitat type may affect prey selection; fish tend to be less selective when foraging in complex environments. Learned responses by the fish may also alter the relative profitability of prey types, as prior experience with prey types reduces handling times. Prey selectivity may even change over the course of a single foraging bout. Fish tend to be less selective if they are hungry and become more selective as they feed. These factors are often overlooked, but could have important effects on tests of foraging models because they indicate that preferences for prey are highly dynamic. Possible physiological correlates of prey selectivity have not been investigated thoroughly, but there are numerous possible research avenues in this regard. For example, it could be hypothesized that fish with increased metabolic requirements (increased SMR) may be less selective when foraging.

Ontogenetic Diet Shifts

The diet of fish larvae is restricted to the smallest zooplankton, but as they grow, increased mouth gape size and swimming ability can allow for the capture and ingestion of a wider range of prey types. The ingestion of larger prey and increased feeding opportunities allow for increased growth, which in turn allows for the ingestion of even larger prey, and so on. Meanwhile, smaller prey that were once dietary staples may not be consumed at all once fish reach a larger size because of the relatively low energetic value that they provide. Such changes in diet with growth and development are widespread among fish species (**Figure 3**).

Many piscivorous fishes are planktivores as larvae, shift to feeding on benthic prey, and then reach a large enough size to begin feeding primarily on fish. In addition to gape size, an important driver for ontogenetic diet shifts may be changes in metabolic demand during ontogeny. If fish are unable to access larger prey during ontogeny, they can become growth stunted or show decreased body condition. Energetic demand can also change abruptly at certain points during development independent of size (e.g., during metamorphosis), and such changes in metabolism might necessitate changes in diet.
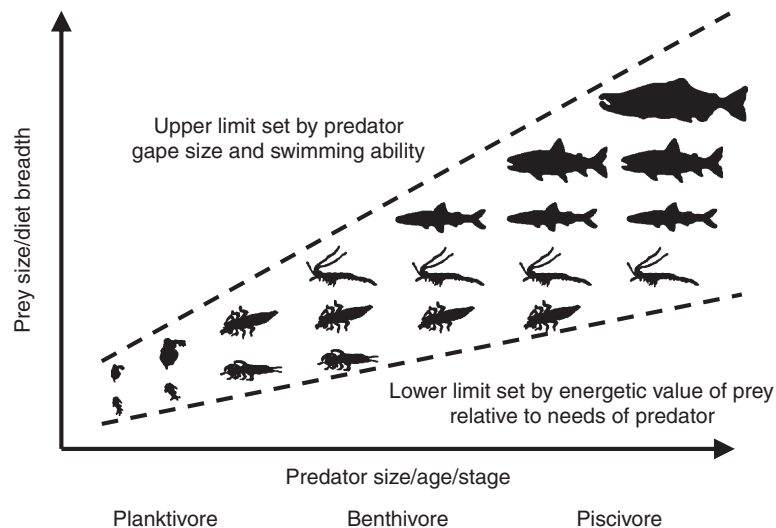
Figure 3 Shifts in diet during ontogeny. As fish grow and develop, increased gape size and improved swimming ability allow for the capture and consumption of a greater range of prey types. Adapted with permission from Brett Johnson (http://welcome.warnercnr.colostate.edu/class_info/fw300/flashcrd/ontogeny.gif).

More on Prey Handling

Costs of Prey Pursuit and Capture

Maneuvering while chasing prey is more costly than is swimming at a fixed velocity. Juvenile Atlantic salmon in streams are less willing to travel across prevailing currents to intercept drifting prey at increased flow velocities. One reason why prey pursuits are costly is because they often require inefficient burst-type anaerobic swimming. Interestingly, the anaerobic capacity of fish may adapt to their diet. For example, fish that regularly feed on larger prey develop higher concentrations of white muscle lactate dehydrogenase (an important enzyme required for anaerobic metabolism) than those that feed only on smaller prey. This change in muscle biochemistry probably helps prepare these predators for the increased anaerobic performance required for pursuing larger fish. Though it usually does not require an anaerobic contribution, even filter feeding on planktonic prey is costly, because fish must swim constantly with increased drag caused by the flaring of the operculae and movement of water past the gill rakers. For larval fish, the costs of pursuing prey are substantial because the vast majority of larvae are active foragers and must overcome disproportionately large amounts of viscous drag due to their exceedingly small body size.

Prey Orientation and Ingestion

Piscivorous fishes most often attack prey by biting the head and swallowing the prey headfirst. There are a few species (e.g., pike, walleye *Sander vitreus*, and rainbow trout *Oncorhynchus mykiss*) that preferentially attack prey at the tail or middle of the body, but even these fish usually rotate the prey to be swallowed headfirst. This alignment reduces buccal and esophageal abrasion, because any spines protruding from the prey fish will be pushed down instead of outward. From an energetic perspective, headfirst attacks are advantageous for two reasons. First, they reduce overall handling time because the prey does not need to be re-oriented after capture (which often involves repeatedly ejecting and recapturing the prey). Second, rates of escape are increased when attacking the tail. This is especially true when attacking large prey, and piscivores feeding on larger species attack the head more often than when feeding on smaller species.

Some species switch between alternate foraging modes when capturing and ingesting prey. For instance, some species (e.g., American eel *Anguilla rostrata* and bluefish *Pomatomus saltatrix*) will either swallow their prey whole or, for larger items, tear the prey into pieces before ingesting the individual parts. In addition, several Chondrichthyan species (e.g., sawfish *Pristis* sp. and thresher shark *Alopias* spp.) use modified body parts as weapons to stun or injure prey, thus making them easier to subdue and consume. These modes of capture and consumption can allow a species to increase its dietary breadth, but are also energetically costly. Therefore, they are generally only used when prey that are small enough to be easily captured and swallowed whole are not available.

See also: **Cellular, Molecular, Genomics, and Biomedical Approaches**: Growth Hormone Overexpression in Transgenic Fish. **Energetics**: General Energy Metabolism. **Food Acquisition and Digestion**: Cost of Digestion and Assimilation; Dietary Requirements of Fish Under Culture Conditions. **Gut Anatomy and Morphology**: Gut Anatomy. **Hypoxia**: Metabolic Rate

Suppression as a Mechanism for Surviving Hypoxia. **Integrated Function and Control of the Gut**: Endocrine Systems of the Gut. **Integrated Response of the Circulatory System**: Integrated Responses of the Circulatory System to Hypoxia. **Social and Reproductive Behaviors**: Dominance Behaviors. **Swimming and Other Activities**: Cellular Energy Utilization: Environmental Influences on Metabolism; Energetics of Fish Swimming. **Temperature**: Membranes and Temperature: Homeoviscous Adaptation. **Tissue Respiration**: Mitochondrial Respiration. **Ventilation and Animal Respiration**: The Effect of Exercise on Respiration.

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