Food and Feeding

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7.1 Introduction

The great phyletic and ecological diversity of fishes discussed in earlier chapters, are reflected in the many types of food utilized by fishes as well as their many ways of acquiring food. Although most fish are classified as food generalists or opportunists, eating whatever they can which is most abundant and easily available, as does the blue shark (*Prionace*), which feeds on dead whales, fish, cephalopods, adult ascidians, gastropods, and crabs, some possess extreme specializations that permit feeding in what may seem to us to be most bizarre ways. For example, insectivores such as the archer fish (*Toxotes*) knock insects off overhanging vegetation by squirting a jet of water at them, while the much larger *Osteoglossum* leaps up to 2 m out of the water to snatch them off branches.

In a fascinating study of the cichlid fishes of the African Great Lakes, Fryer and Ilies (1972) discuss the many ways of cichlid feeding. Cichlids possess an array of morphological features, including jaw structures, mouth size, and shapes, dentition, and gill raker size and number, which allow them to occupy an even wider variety of feeding niches. Besides the typical filter, plankton picking and predatory feeding niches seen in other fishes, cichlids illustrate a number of unique feeding niches including such extraordinary specializations as head-ramming in order to dislodge scales from the sides of other fishes or even eggs or larvae that are being transported in the mouth of mouth-brooding parents, shamming dead on the bottom to decoy other fishe s, and as in the Malawi eye-biter, *Haplochromis compressiceps*, sucking the eyes out of other fishes. Cichlids also provide some of the best examples of cleaning behavior among freshwater fishes (Stauffer, 1991) and scraping "aufwuchs" (an algal and detrital biolayer) from the surface of rocks (Fryer, 1959) The freshwater cichlids as well as the marine wrasses and parrot fishes (Labridae, *sensu latu*), embiotocids (surfperches), pomacentrids (damsel fishes), and odacids (Eastern Pacific butterfishes) have sometimes been classified together based on the similarity of their feeding apparatus. Although the monophyly of this grouping has been challenged by molecular evidence, these so-called labroid fishes continue to represent the epitome of feeding diversity. According to Peter Wainwright (2005) at the University of California at Davis, feeding diversity among labrids is unparalleled among reef fish groups and is associated with high mechanical diversity in the jaws. The complex lever systems of their jaws have permitted the evolution of a wide range of physical and mechanical variation permitting a variety of feeding styles from picking parasites from the sides and gills of larger fish to capturing small invertebrates and fishes from a distance (as best illustrated by the aptly named slingjaw wrasse, *Epibulus insidiator* (Figure 7.1), in which the mouth can be thrust forward nearly 50% of the body length) to consuming relatively large prey such as heavily shelled molluscs and crabs. Within the Labridae, some parrot fishes exhibit a unique jaw apparatus which with their fundamentally different tooth morphology may explain the greater taxonomic, morphological, and mechanical diversity of parrot fishes in contrast to the wrasses *per se*. (Wainwright *et al.*, 2004).

The study of the feeding apparatus and mechanics of fishes provides some of the best examples of the adage “form follows function,” or as might also be said, “you are what you eat.” These similarities in morphology cross phylogenetic lineages, as Norton and Brainerd found in their 1993 study – buccal and opercular pressure profiles were more similar in ecomorphologically similar feeding styles than in species that were closer related but possessed different feeding styles (e.g. predatory cichlids and basses vs. picking cichlids and sunfishes).

Rather surprisingly perhaps, although some fishes seem to have specializations that suggest a particular diet and mode of feeding, this does not prevent them from turning these adaptations to other uses.

Thus, the cichlid *Petrotilapia* of Lake Malawi is seemingly specialized for scraping algae off rocks with its trifid teeth, but Liem (1980) found that it could also feed in seven other ways, each involving a different pattern of jaw muscle activity. For instance, *Petrotilapia* bites scales and fins from other fishes, collects floating food, sucks invertebrates from bottom mud, and catches small fishes in midwater (Figure 7.2). This kind of versatility in using what seems to be a morphology adapted for a single purpose may be uncommon, but it is a salutary warning to anyone attempting to interpret function from morphology alone!

7.2 Techniques for Studying Food Habits and Feeding

While most early studies of fish feeding involved capture and subsequent dissection to examine stomach contents, killing fish may be undesirable because of ethical considerations and possible population impacts (Kamler and Pope, 2001). Two non-lethal methods that are widely used to collect stomach contents from living fish are stomach tubes and pulsed gastric lavage. The former is a simple tube, usually glass or plastic, inserted through the esophagus of an anesthetized fish. Stomach contents are then removed by suction or compression of the sides of the stomach. Gastric lavage uses pulses of water, in connection with a tube, to flush contents from the stomach and is generally regarded as a more efficient technique. The use of antibodies, stable isotope ratios or nucleic acids (Rosel and Kocher, 2002) can be used to identify accurately even well-digested foodstuffs.

Fish biologists today have come to rely on various high-tech devices and techniques to advance our understanding of feeding mechanisms. Under - water observation of feeding behavior may be recorded digitally or photographically. Data from EMG recordings, pressure transducers and fiber-optic endoscopes are combined with computer models to study and describe how food is handled and processed prior to its being swallowed (Ferry-Graham and Lauder, 2001). Digital particle image velocimetry (DPIV) utilizing lasers to illuminate reflective particles suspended in the water allow the visualization of water flow patterns inside of the fish’s mouth (Higham *et al.*, 2006). High speed digital photography then shows the actual patterns of water movement that result from feeding activities.

7.3 Optimal Foraging Theory

In recent years, ecologists who are interested in how organisms exploit their environment have developed a theory of *optimal foraging*, which basically states that organisms will preferentially feed on food resources that provide the greatest long-term net nutrient return for the least energy investment or risk on the part of the consumer. Energy may be invested in finding food, capturing it, ingesting it, and finally digesting and absorbing its nutrition. Risk involves chiefly exposure to predation although some prey species possess defensive abilities that test their predators. Optimal foraging theory is subject to debate; however, actual observations on different feeding strategies tend to support it. What is not debatable is that fish must acquire enough energy from their food to survive and to reproduce.

7.4 Food Choices, Size, and Development

But optimal foraging strategies may not remain identical throughout an organism's lifespan and many species exhibit a *trophic ontogeny* or shift in food types and sizes, or feeding styles at different stages in their life cycle. These are necessitated by the fishes own increase in size, by morphological developments or by habitat shifts that accompany growth (Figure 7.3). Adult fishes consume a great variety of foods and exhibit a great variety of feeding styles, although basically all feeding mechanisms may be categorized as either biting, ram feeding, or suction feeding based on how food gets into the mouth. Different types of food are then concentrated and processed for "swallowing" by several methods. Foods range in size from microscopic phytoplankton, bacteria, and detritus, through a progressively larger series of zooplanktons, and culminating in larger invertebrates and other vertebrates. Some fish also consume multicellular algae and vascular plants.

Although in general there is a positive correlation between the size of a fish's mouth and the size of the prey it consumes, there are some notable exceptions. Some of the largest fishes, for example whale sharks (*Rhincodon typus*) and basking sharks (*Cetorhinus maximus*), use their huge mouths to engulf and filter large quantities of small organisms. But what is "small" can be relative – a 20 meter whale shark may filter feed on juvenile tunas that are themselves 25–30 cm in length. At the other end of the size range of sharks, the diminutive 15–50 cm cookie-cutter sharks *Isistius brasiliensis* and *I. plutodus* feed on whales and other large oceanic creatures, although they do so one small bite at a time (Figures 7.4A, B).

7.5 Food Capture

According to Karel Liem (1980) most of the enormous variety and range of foods eaten by fishes is obtained through only three basic feeding styles: ram feeding, suction feeding, and manipulation or biting. Virtually all species use one, and, because they are not mutually exclusive, most species use two of these styles.

Much of the evolutionary change that has occurred in lineages leading to both modern sharks and bony fishes has involved the development of mouths and jaws that are more efficient in food gathering. Primitive Actinopterygians (Paleoniscoids) as well as living polypterids provide examples of jaw structures that are adapted to engulfing their food whole. The relatively inflexible jaws of these older lineages were limited to more-or-less opening and closing and contrast sharply with the protrusible jaws of modern teleosts that actually reach out to engulf their prey (Lauder, 1980a, b). Jaw protrusion is believed to have evolved independently at least five times: in sharks, in chondrosteans, in ostariophysans, and again in higher teleosts (chiefly acanthopterygians, but also in cods (Gadidae) perhaps uniquely among the paracanthopterygians).

A key factor in the evolution of protrusible jaws in the acanthopterygian perciform lineage has been the increased importance of a highly mobile premaxillary and commensurate restriction of the maxillary as the primary structure in the upper jaw (Ferry-Graham and Lauder, 2001).

These fishes open their mouths by utilizing the hypaxial/sternohyoideus muscle to lower the mandible, but can also use their epaxial muscles to hinge the neurocranium upwards relative to the vertebral axis and thus increase the size of their gape (Figure 7.5). In its simplest form, expansion of the buccal cavity is very limited in these cases and a small, but adequate, negative pressure is developed; however these fishes may enhance their feeding efficiency by ram feeding – using body velocity to overtake and capture prey.

Although ram and suction feeding may be viewed as extremes of a spectrum of feeding modes (Norton and Brainerd, 1993), many fish use a combination of forward motion of the body or jaw in addition to generating suction pressure to entrain prey. Barracuda (*Sphyraena barracuda*), pike (*Esox*), and gars (*Lepisosteus*) typically rely entirely on ram feeding, engulfing their prey by making a rapid lunge with their jaws wide open (Porter and Motta, 2004). The long-jawed butterflyfish (*Forcipiger longirostris*) rapidly extends its jaws while enlarging its gill chamber and reaching out, often into confined spaces where suction feeding alone would not be as effective. (Ferry-Graham *et al.*, 2001).

Ram feeding occurs when a fish swims with its mouth open through a concentration of food. The mouth may be held open continuously (or for very long periods) or intermittently. Food may then be sieved from the water by gill rakers, collected in sticky mucus, or otherwise routed into the esophagus where it is then swallowed.

Ram feeding is sometimes referred to as “passive feeding,” however, the fish must actively expend energy for swimming and a streamlined fish swimming with its mouth open loses much of its hydrodynamic efficiency thus increasing the cost of swimming and making ram feeding much less energy efficient than it might at first appear to be. This hydrodynamic loss may be partially compensated for by the injection of water from the gill openings into the boundary layer similar to what happens during respiration (see Chapter 5). Studies on herring and other species have shown that a fish may use ram feeding at high concentrations of plankton, but switch to “picking” individual prey (suction feeding) at lower concentrations. At moderate concentrations, when prey would be equally available by either means, fish often favor picking over ram feeding, suggesting that suction feeding is energetically more efficient (Gibson and Ezzi, 1992).

In contrast to ram feeding, most fishes use suction to ingest their prey. The buccal and opercular chambers expand, drawing water, and any prey organisms in that water, into the fish’s mouth.

Suction feeding is used to capture many different types of foods, for example: suspension feeding on dense aggregates of microorganisms or detritus, plankton picking, crevice feeding, bottom vacuuming, and by sit-and-wait predators. Suction feeding typically consists of four phases: (1) preparatory – a decrease in volume of the mouth by compression of the head and elevation of the hyoid; (2) expansive – which occurs progressively from front to rear, beginning with the opening of the mouth and subsequent enlargement of the gape, depression of the hyoid, abduction of the suspensorium, and abduction of the operculum (during which the opercular opening remains closed to prevent the escape of water); (3) compressive – closing of the jaws, adduction of the suspensorium and protraction of the hyoid, while opening the opercular flap; resistance of the gill arches delaying the outflow of water and permitting retention of food; and finally (4) recovery – a return to conditions preparatory for phase 1 (Horn, 1998).

Suction feeding occurs in a wide variety of fishes, and has been suggested as the primitive feeding style for all bony fishes (Hulsey *et al.*, 2005). The absence of teeth associated with the earliest fossils from the Lower Silurian (420 mya) suggests to some that these were also filter feeders. Functional convergence in suction feeding between living sharks and bony fishes reflect similar hydrodynamic constraints resulting from evolutionary pressures to develop greater feeding efficiencies through protrusible jaws in both lineages.

Relationships between jaw suspension and feeding in sharks are not, however, as clear as formerly believed (Wilga, 2002). Upper jaw protrusion in elasmobranchs (Figure 7.6) is related to morphology of the upper jaw-chondrocranium articulation rather than to the type of jaw suspension as had been previously suggested. Interestingly, the same jaw morphology and musculature that permits suction feeding can also be adapted to allow the fish to eject a stream of water that can be used to uncover buried prey or manipulate prey so it can be more easily consumed. Dasyatid and myliobatid stingrays forage by jetting water out of their ventrally oriented gill openings to blow large pits in the bottom (Wilga *et al.*, 2007), and these have been recognized in fossil sediments. The ability of archer fish (*Toxotes*) to "shoot down" insects with jets of water has already been mentioned and triggerfishes (Balistidae), which feed on echinoderms, use a jet of water to uncover buried sand dollars or overturn long-spined sea urchins, allowing them to attack the undefended ventral side.

Biting, as defined by morphologists and biomechanicists, involves the use of the jaws to grasp prey and includes feeding on only parts of a larger prey organism, taking bites of flesh, or of fins, scales, eyeballs, parasite picking, or benthic scraping found in many species of coral reef fishes and rock-dwellingcichlids in which the jaws are applied to the substrate or directly to the prey.

When defined this way, biting becomes the most specialized mode of feeding, and is believed to have evolved several times: in sharks (and perhaps earlier in placoderms), in cichlids, plectognath fishes (triggerfishes and their relatives), and in algal scrapers in diverse families including loaches, catfishes, blennies, and cichlids.

Regardless of the mode of feeding the feeding apparatus of most fish consists of four-bar-linkage systems constructed from the bones of the skull that form an expandable mouth cavity shaped like a truncated cone (Figure 7.7A–C). In contrast to simple lever systems, such as the lower jaw, most of which possess an input and an output link that rotate around a fulcrum provided by the jaw joint, four-bar linkages have a third link that transfers the transmission of motion and force as well as a fourth, stationary, link that anchors the assembly. Four-bar linkages are found not only in the mouth but also the pharyngeal and opercular apparati and these multiple linkages work together to permit the capture and processing of food. Expansion of the mouth cavity produces negative (suction) pressure that assists in the ingestion of food. Naturally, the actual feeding mechanism of fishes is more complex than this simple model and differences in the relative sizes and position of each bony element in the linkage system as well as associated muscles and tendons can produce a great variety of results, ranging from very rapid and forceful to very slow and precise feeding movements (Higham *et al.*, 2006; Figure 7.8). Most suction feeders are inter - mittent, however, lampreys and their ammocoete larvae possess anatomical structures that permit more-or-less continuous suction feeding currents.

7.6 Handling and Ingestion

Once food is captured it must (except in aerial and terrestrial feeding species) be separated from the water, transported to the rear of the mouth and oriented in such a way so that it can be swallowed or ingested. Fishes that feed on larger prey make use of the hydrodynamic properties of their oral chambers to insure that the food is moved towards the esophagus and does not escape through the mouth or gill openings. After food is taken in through the mouth, expansion of the mouth and gill chambers creates a movement of water that continues to transport food toward the rear of the mouth. Food transport may be assisted by teeth on the tongue and palate, or by the gill rakers. Although the same muscles and bones are used for food capture and handing, experimental results demonstrate that handling is a distinct process, although obviously one that is closely tied to food capture.

Versatility of the expanding cone model is restricted not only to prey capture. Pressure differences in different areas within the cone can be generated by modulating muscle actions. In this way captured prey can be moved or turned within the cone – it acts as a hydrodynamic tongue.

Suspension feeding occurs when water laden with microscopic organisms or detritus is drawn into a fish's mouth. These particles can then be removed by filtration or sieving, trapped in sticky mucus, or by other means that are not fully understood. Apparently, fishes have been utilizing this method for nearly as long as there have been fishes. Not only do the living cephalochordates feed this way, but studies done on the feeding apparatus of jawless heterostracans indicate that they were primarily suspension feeders. But this is not to say that modern fish feed in an identical manner. Suspension feeding occurs in 11 orders of fishes, and is found in many of the world's economically important species. Traditionally, filter and suspension feeding were thought to be associated with ram feeding, however, recent work shows that suction pump feeding plays an important role. Along with the whale shark and the megamouth shark (*Megachasma pelagios*), the basking shark is one of three species of large, filter-feeding sharks (Figure 7.9). However, it, together with the manta and devil rays (*Mobula*), is the only elasmobranch that relies solely on the passive flow of water forced through the pharynx by swimming. In contrast, the whale shark and megamouth assist the process by suction or actively pumping water into their pharynxes. Not only whale sharks but various bony fishes also draw water into their mouths at higher velocities than in passive filter-feeders, enabling them to capture larger more active prey as well as larger aggregations of zooplankton.

Varied methods are also employed to separate food from the water. As it turns out, fish do not swallow much water with their food, so somehow food and water are separated. In many fishes the muscular esophagus or oropharyngeal sphincter, which separates the esophagus from the pharynx, serves to prevent the passage of too much water, in some cases probably wringing unnecessary water from the food as it being swallowed. In recent years several studies have demonstrated that the classic view in which food is sieved from the water by the gill rakers is inadequate. In the classic model, the gill rakers serve as a mechanical sieve, trapping food as the water flows between them (Rubenstein and Koehl, 1977; Silvester, 1983). Particles that are too large to pass through the pores defined by the rakers, or by microbranchial processes, small projections that extend out from the rakers, are trapped on lateral gill rakers, and are then passed forward to the medial rakers of the preceding arch before being transported posteriorly to the esophagus. Channel size may be varied by bony tips of medial gill rakers on the preceding arch, which are moved into the inter-raker channels; but not all fish have this ability. Alternate sieving models suggest that the upper surface of each branchial arch between the rakers forms a functional sieve, not the rakers themselves (Van Den Berg *et al*,. 1994). For example the numbers of gill rakers increase in young herring up to 50 mm in length, however, above 50 mm length the increase dramatically slows. The length of the gill rakers and the distance between adjacent rakers increase throughout life making a constant sieve size based on inter-raker distance impossible, however, the area provided along the length of the rakers increases proportionally to the fish’s size (and food requirements).

But food may also be effectively separated from the water by methods that do not involve mechanical sieving. The gill arches cause a swirling vortex to form at the roof of the mouth in some species. Food particles are trapped in the vortex, stick to mucus on the roof of the mouth and are then swallowed. Plankton filterers and detritivores such as the thread-fin shad (*Dorosoma*) and the anchovy (*Ctengraulis*), both clupeoids, the osteoglossid (*Heterotis*), the milkfish (*Chanos*), and mullets (*Mugil spp*.) possess paired epibranchial organs, muscular diverticula containing mucus cells at the back of the pharynx which probably squeeze concentrated food particles into a bolus before swallowing.

Aerosol (or hydrosol) filtration, separates particles using adhesive properties of the filter elements, rather than pore size. The mucus covered surfaces of the arches themselves may serve as the sites of filtration with inter-raker spaces serving only for the removal of water from the oral chamber. Alternatively, the barrier formed by the rakers may act as a crossflow filter. Crossflow filtration is widely used in industrial applications such as winemaking, brewing, and water purification. It is a valuable method for filtering large volumes without clogging filters. Instead of passing a mixture of water and food particles through the filter, the mixture is passed across the surface of the filter. In a process that is not well understood, the liquid is drawn through the filter, while solids accumulate on the "downstream" end of the filter where mucus entrapment may also help in capture and retention of food particles (Figure 7.10). Both aerosol and crossflow filtration could possibly reduce the energetic costs of feeding since there is reduced hydrodynamic resistance and no clogging to overcome (Sanderson *et al*., 2001).

Thus, mesh sieving is only one of numerous mechanisms described by engineers by which solids may be separated (filtered) from a suspending fluid. It appears that fish may use most, if not all, of these, with more than one mechanism occurring sometimes in a single species or even an individual, depending on the size and concentration of the food.
Carp sieve out larger food particles (insects, etc.) while using crossflow filtration, not sieving, to concentrate smaller (detrital and microbial) food particles. At the same time, similarly sized inorganic particles are expelled through their opercular openings or by spitting through a process known as oral winnowing. Oral winnowing is the separation of food from non-edible materials, and occurs when the flow of water reverses within the mouth cavity. During winnowing, only a little of the water escapes through the mouth. Most, together with the indigestible materials, is forced out of the opercular openings or the mouth during a subsequent contractile effort.

7.7 Anatomy and Physiology of the Digestive Systems

The capture, processing and reduction of prey into nutrients is the function of the digestive system which can be thought of as a series of interconnected tubes through which food passes, each with specialized anatomical and physiological features, and associated secondary organs that provide the means of mechanical and chemical digestion, absorption of nutrients, and the final elimination of undigested materials. Beginning anteriorly, these organs are the mouth and oropharynx with its teeth, gillrakers and other structures for the initial capture and ingestion of food, the esophagus, the stomach, the intestine with its associated digestive organs: the liver, pancreas, and gall bladder, and last the rectum, or in some fish a spiral valve. The operation of the digestive system is under direct and complex control systems of hormones related to food ingestion and movement through the gut. The production of these hormones makes the intestine the largest endocrine organ in the body (Chapter 9). In addition to digestive functions, the intestine, especially the posterior portions, plays an important role in excretion and immune functions, as discussed in the appropriate chapters.

Teeth

Living Agnathan fishes possess conical, rasping tooth-like structures made of keratin, the same structural protein found in human hair and nails, on their tongue, rather than enamel covered, bony teeth typical of other vertebrates (Figure 7.11). The lamprey also has similar teeth around its mouth. They also have no identifiable esophagus or stomach. The intestine is straight with little regional differentiation, although parasitic/predatory lampreys have a single fold (typhlosole) that runs in a spiral along the length of the intestine increasing the absorbent surface. In non-parasitic lampreys such as the North American and British brook lampreys (*Lampetra appendix* and *Lampetra planeri* respectively), some North American species of *Ichthyomyzon*, and the southern hemispheric *Mordacia praecox*, the larval stage persists for several years as a filter feeder and following metamorphosis the adult digestive system is non-functional and no food is consumed from when they metamorphose until they spawn and die one-half year later. An intermediate condition is found in the non-parasitic Caspian Sea lamprey, *Caspiomyzon wagneri*. Ammocoete larvae live in bottom deposits and feed on diatoms and detritus, however, adults feed on algae and higher plants as well as scavenging dead fish and are known to attach themselves to trout, presumably for transport.

Jawed fishes possess many types of teeth both in their jaws and elsewhere in their mouth cavities. Jaw teeth located on the premaxillary, maxillary, and mandible (dentary) are used for biting, grasping, shearing, rasping, or scraping.

Depressible teeth allow food to move into the mouth but not outwards. Many fish possess only small pointed teeth suitable for immobilizing prey while relying on suction mechanisms to finish the job of prey ingestion. Barracuda and similar predatory species possess large, shearing teeth that cut their prey nearly in two, allowing it to fold for easier ingestion. The bladelike teeth of predatory sharks are justifiably celebrated for their ability to remove "chunks" of flesh from large victims (Williams, 2001). In addition, or sometimes instead of jaw teeth, many fish possess teeth on their tongue or the roof of the mouth (palatine and vomerine teeth), which also help hold food and direct it to the esophagus. One entire major group of fish derives its name from the presence of teeth on their tongues; the Osteoglossomorpha, a name which translates as "bony tongues." Pharyngeal teeth located on, above, and below the pharyngeal arches are important for shearing or crushing prey. They often occur in fish that otherwise lack teeth, such as carps, minnows, and suckers; however, many families such as parrot fish, cichlids, and drums possess pharyngeal teeth in addition to well developed jaw teeth. As illustrated by drums that feed on hard-shelled mollusks, the form of pharyngeal teeth may change with growth, cardiform teeth found in small fish which feed on softer-bodied prey are replaced by villiform teeth, which in turn are replaced by heavy molariform teeth as the size class of drum and the hardness of their favored prey increases.

The digestive tract

The digestive tract of fishes is divided into four regions: the foregut (esophagus and stomach, if present), mid-gut, hindgut, and rectum. The foregut begins at the posterior boundary of the gill cavity or pharynx and includes the esophagus, the stomach, when present, and the pylorus.

Typically, the esophagus is a short muscular tube connecting the oropharynx with the stomach. Often the esophagus can expand to accommodate almost anything a fish can get in its mouth. In marine and euryhaline fishes such as tilapia, eel, and flounder, the esophagus also plays an important role in maintaining water balance, serving as a site for the absorption of water imbibed by the fish in order to offset osmotic loses to a hypertonic environment (see Chapter 6). Fishes of the order Stromateidae often possess pharyngeal sacs that may or may not be equipped with tooth-like projections. Many of these species feed on soft-bodied coelenterates.

A stomach may be present or absent. In its simplest form, the stomach is an elastic sac that receives and stores food, and begins chemical digestion; however, in mullet, *Corregonus*, *Sardinella*, or *Mormyrus* – most of which are microphagous detritivores or herbivores – part of the stomach may be modified into a gizzard-like structure (Figure 7.12).

Fishes which lack stomachs include Holocephalans, which typically feed on mollusks as well as some fish; lungfish, which are predatory on fish, mollusks, and arthropods, barnacle eating blennies, and a variety of herbivorous fishes.

In most fishes the esophagus enters the stomach anteriorly and the intestine exits posteriorly (Figure 7.13A). Typically, there is no anterior (esophageal or cardiac) sphincter, however, most fish possess a well developed pyloric sphincter that regulates the passage of partially digested food from the stomach. An interesting variation on this basic design is found in the Lake Magadi tilapia (*Alcolapia grahami*) that dwell in extremely alkaline waters (Bergman *et al.*, 2003). In this species the intestine connects directly to the esophagus and the stomach at a three-way junction formed rather like an upside down letter “T” (Figure 7.13C). When the stomach contains food, the pyloric sphincter will close, permitting alkaline water to pass directly into the intestine, and thus preserving the acidic environment of the stomach. A somewhat similar situation is found in other tilapine cichlids in which the pyloric sphincter is located anteriorly in the stomach, but not in direct opposition to the esophagus (Figure 7.13B).

The stomach is a site of protein digestion initiated by the enzyme pepsin. Hydrochloric acid (HCl) secreted by gastric glands provides proper pH for pepsin, and also serves as a chemical barrier to bacteria and parasites. It may also assist with the breakdown of hard, shelly materials. The stomachs of many fishes also exhibit chitinase activity, although whether this enzyme is secreted in the stomach or esophagus or both is not clear.

The remainder of the gut is differentiated into regions, but what the physiological role is of each is not clear. Aside from the obvious roles in digestion and absorption of nutrients, posterior sections also play roles in salt and water balance and immunity.

The mid-gut includes the intestines posterior to the pylorus, and often merges without anatomical distinction into the hindgut, although, in some fish, the beginning of the hindgut is marked by an increase in gut diameter. The mid-gut often includes a variable number (from zero to 1000) of pyloric caecae near the junction of the stomach and intestine. Pyloric caecae occur in fishes of almost every feeding variety and their function is not clear. It has been suggested that they serve to increase surface area or as sites for the absorption of certain nutrients (fats and waxes; Buddington and Diamond, 1986). They have been shown to contain digestive enzymes including pepsin which has a pH optimum of about 1.5–4, which is certainly not typical of intestinal pHs (Horn, 1989). Pyloric caecae are always absent in fishes that lack stomachs. The mid-gut is typically the longest portion of the gut, ranging from less than one body length to over 20 body lengths and may be coiled into complicated loops (often characteristic for each species) when longer than the visceral cavity. The length and complexity of the mid-gut often provides a clue to the feeding habits of the species (de Groot, 1971), however this relationship is not infallible.

The remainder of the digestive tract may be differentiated into a hindgut and a rectum, and at the posterior end the hindgut exits the body cavity via the anus or cloaca; a chamber formed from infolded body wall, receiving both the anal and urogenital openings which occur in sharks, rays, and Sarcopterygians, but never in teleost fish or holocephalans. A pre-rectal ileorectal valve may be present, as in many teleosts, and some fishes also possess a single large hindgut caecum which may be used as a final site for digestion and absorption (*Polypterus*), fermentation of herbivorous materials or even as a respiratory chamber (Gee and Graham, 1978).

Digestive enzymes

Like other animals, fish possess an array of digestive enymes by which large macromolecular nutrients are broken down into smaller molecules that can be assimilated. Most fish possess seven main digestive enzymes – trypsin, maltase, amylase, two +aminopepsidases (carboxypepsidase a, carboxypepsidase b), lipase, and alkaline phosphatase. Almost all the major enzymes are present in all fish regardless of their food habits, however, the relative concentration and activity varies according to food preference. Pepsin is localized in the stomach where it functions at optimum pHs between 1 and 4, while the others are found in the intestine at more alkaline pHs. The optimum pH for each enzyme varies with different regions and between different species. In general, the optimum pH for trypsin lies between 6.8–7.8, for carbohydrases 5–7, and for lipases the most alkaline > 7.8. There are two sources of enzymes for the mid-gut – the pancreas and the secretory cells in the gut wall. Since the pancreatic tissue is often diffuse and closely adhering to the liver, portal veins, and gall bladder, it is often difficult to determine the exact origin of many digestive enzymes. Many fish appear to produce amylase and other carbohydrases, but others rely on the activities of gut microflora to supply these enzymes. Chitinase has already been mentioned as occurring in the stomach, but in some fish it is found only in the intestine where it is secreted by the pancreas. Absorption efficiencies of carnivorous and herbivorous teleosts differ significantly.

In carnivorous species the energy absorption efficiency is around 80% (up to 97% for adult sea lampreys feeding on blood), and for herbivores much less, around 40–50%. The only elasmobranchs examined have been lemon sharks (*Negaprion brevirostris*), which have been found to have absorption efficiencies up to 83%. It is interesting that lemon sharks and carnivorous teleosts should have similar energy absorption efficiency values, for the shark digestive strategy is very different to that of most teleosts. Thus, compared to teleosts, these sharks have a low rate of food intake (1% of body weight per day in the sandbar shark, *Galeaspis*), extended retention time, greatly increased surface area – with the spiral valve at the hinder end of the gut – and grow slowly.

Other organs

The pancreas is an important source of digestive enzymes. It may be a discrete organ or a diffuse mass of tissue (Hilliard and Potter, 1988), often interwoven among pyloric caeca. Islet cells, the sources of insulin and glucagons, may be found within the pancreatic mass as is typical of higher vertebrates, or separately, often in association with liver tissues. Endocrine pancreas islet cells are often consolidated into large tissue masses, known as Brockmann bodies. Newly absorbed nutrients are transported to the liver by the hepatic portal vein. The liver, which may be the largest organ besides swimming muscles in a fish’s body, is not directly involved with digestion, but assimilates nutrients, produces bile, and detoxifies toxins from both endogenous (metabolic) and exogenous sources. A final organ associated with digestion is the gall bladder which secretes bile, produced by liver, that aids in emulsification and increases intestinal pH. The gall bladder also excretes absorbed toxins and metabolic wastes back into the gut for elimination.

7.8 Food Types, Characteristic Adaptations, and Feeding Guilds

Suites of characteristics, including anatomical, physiological, and behavioral adaptations, come together to permit fish to best utilize an amazing variety of foods (Wainwright *et al*. 2000). Fishes sharing such dietary specializations are often regarded as belonging to the same Feeding Guild.

Carnivorous fishes

The vast majority of living fishes are predatory. Of some 1100 species of extant elasmobranchs, only 13 (1.2%) – the basking shark (*Cetorhinus maximus*), megamouth shark (*Megachasma pelagios*), whale shark (*Rhincodon typus*), manta ray (*Manta birostris*), and about nine species of devil rays (genus *Mobula*) – have forsaken the actively predacious habits of their kin and adapted to a more placid "grazing" lifestyle.

Predatory (piscivorous) fishes typically have large, terminal or subterminal mouths with well developed grasping and biting teeth. Many also have teeth on the tongue and roof of mouth. Among predatory fishes adapted to feeding on hard, shelly prey some jaw or pharyngeal teeth are usually heavy and molariform. Gill rakers, if present, are typically short or blunt. They have a well defined stomach, and typically possess pyloric caecae. The intestine is relatively short. They may be strong swimmers or sit-and-wait ambushers. And, if the latter, they may possess camouflage, lures and the like.

Some predatory fishes feed on the sea's abundant gelatinous animals such as ctenophores, jellyfishes, and salps. Correlated with a gelatinous diet are enlarged digestive tracts, exceptionally large stomachs, and extremely long intestines. Fish feeding on gelatinous animals also may have pharyngeal or esophageal modifications, presumably to prevent regurgitation (Fänge and Grove, 1979). *Mola mola* has three rows of recurved pharyngeal teeth. In the stromateoid fishes, there are esophageal sacs with denticulate papillae. *Genicanthus personatus*, the masked angelfish, includes hydromedusae and siphonophores in its diet and has finger-like esophageal papillae that point posteriorly. The esophagus of chum salmon is strongly muscular with a well defined sphincter.

Plankton filterers

Another major feeding guild consists of plankton filterers. A successful plankton filterer needs to be able to separate plankton from the water. Typically this occurs through mechanical filtration by means of gill rakers, but, as noted in “Food choices, food and development”, aerosol filtering is employed as well. Some filter-feeders, especially those in which phytoplankton is an important source of food, have exceedingly long guts. The gut in the menhaden is ten times the length of that in the herring and has 400 pyloric caecae compared with 20 in the herring, reflecting the greater difficulty of digesting plant food. Filter-feeding appears during ontogeny; it is not found in young larvae, which are usually microzooplankton particle-feeders. In herring and menhaden, in the paddle fish *Polyodon* and in certain cichlid species filtering appears as the gill rakers develop. Most of the clupeoids must reach a length of 80–100 mm before starting to filter.

Large zooplankton filter-feeders

There are a few large fishes that are able to filter sufficient water to be able to filter-feed on zooplankton when this is abundant. In freshwater, the paddle fish (*Polyodon*) of the Mississippi Basin filters cladocerans, cruising around with its lower jaw dropped almost to 90° (Figure 2.18 on p. 52). In the oceans, the huge whale sharks (*Rhincodon*), basking sharks (*Cetorhinus*), and manta and devil rays (*Mobula*) all filter-feed. In whale sharks and manta rays, the filter is spongy tissue formed from modified denticles, while in basking sharks, there are long gill rakers (again modified denticles; Figure 1.19 on p. 23) on each gill arch. Whale sharks sometimes filter in the vertical position, pushing their heads slowly out of the water, allowing the pharynx to drain, and then subsiding slowly again below the surface. Basking sharks feed on copepods and live in temperate waters, where zooplankton varies widely in abundance during the year.

While early calculations based on assumed zooplankton calorific value and abundance on the one hand, and estimates of the energy expenditure of the shark when swimming with wide open mouth while filtering on the other, suggested that these enormous fish are actually balanced on the knife edge of using more energy capturing their food than they can obtain from it. Several of the assumptions behind these calculations were recently shown by David Sims (1999, 2000; Sims *et al.*, 2003) to be faulty, resulting in an overestimation (by about three times) of the energy basking sharks require to swim. Also, contrary to earlier reports, basking sharks (although not all of them) do not shed their gill rakers and hibernate in the winter, but instead they feed on deeper-dwelling populations of mesopelagic zooplankton that do not experience such dramatic seasonal variations in abundance. However, at least some sharks do shed their gill rakers; one stranded at Polperro in Cornwall in November had the rakers covered with epithelium and shorter than those of feeding adults.

Plankton pickers or particle feeders

Particle-feeding or picking zooplankton is seen also in some rather unexpected fishes. The deep-sea tripod fishes (see Figure 2.9 on p. 44) pick copepods from the benthopelagic plankton, as they sit perched on their fins facing into the current. Curiously, the spur dog (*Squalus*) may also feed in this way on the planktonic ctenophore *Pleurobrachia*, which it sometimes takes in such amounts as to fill its gut, and it has recently been suggested (from their parasite communities) that eels of all sizes in rivers and lakes in England feed regularly on planktonic copepods.

Bottom feeders, detritivores

Many detritivores are bottom vacuumers/suckers that typically possess small, undershot, inferior mouths equipped with suctorial lips and barbels, sensory pits, etc. positioned to help detect buried prey. Other detritivores feed on phytoplankton and mud particles, triturated by the same kind of gizzard as in mullets (Mugilidae). Although mullets typically browse on the algal film over mud (leaving a characteristic series of depressions where they have gulped in surface mud), they can also feed on planktonic algae at the surface–air interface using the gill rakers as a sieve (Figure 7.14). Detritivores may have either a oneor two-part stomach. Those with two-part stomachs have short intestines and those with a one-part stomach, a long intestine.

Herbivorous fishes

Herbivorous (phytophagous) fishes generally have small, often inferior, mouths equipped with rasping or nipping teeth. Pharyngeal teeth may be present. Stomachs are generally absent, but if present are thin walled and elastic. Because plant material is usually difficult to digest they may use cellulase and other enzymes produced by gut microflora (Jobling, 1995), hind gut fermentation by bacteria and protozoans of carbohydrates to short-chain fatty acids that can be directly absorbed with intervention of bile salts, or mechanical processing (trituration) by a muscular stomach/gizzard or mastication by pharyngeal teeth.

Overall, herbivorous fishes are very much in the minority, and are least common in the sea and in temperate freshwaters. Only some 5% of all fish families (18 marine and at least 20 freshwater) contain herbivores, although herbivorous individuals may be among the most numerous in any fish community (Horn, 1989). Perhaps this is because although more energy has to be expended by herbivores than by carnivores in obtaining their food, herbivo- rous food resources tend to be quite abundant.

Certainly, compared with carnivores, herbivores have to spend a good deal more of their lives feeding.
Some phytoplankton feeders filter continuously, while a parrot fish spent 8 h day –1, and *Haplochromis* and *Tilapia* 14 h day –1, this in comparison with 1–3 h day–1 for salmonids. Whatever the diet, all fish have a high protein requirement (around 50% of dry weight of the diet). How do herbivores satisfy this requirement?
As detritivores and herbivores they ingest large amounts of attached protein-rich microorganisms, even if they do not eat protein-rich algae.
Most marine herbivores are found around the coral reefs of the tropics, where surgeon fishes (Acanthuridae) crop algae growing over corals and on sandy patches near the reef, while parrot fishes (Scaridae), rabbit fishes (Siganidae), and damsel fishes (Pomacentridae) browse algae scraped off coral surfaces. Some temperate shore fishes, such as blennies and gobies, feed largely on seaweeds, and the much prized temperate freshwater ayu (*Plecoglossus*) of Japanese rivers, feeds solely on moss scraped from its territory of mossy stones. Ayu are an expensive delicacy since they are caught in a curious and somewhat inefficient way; fishermen place a small ayu on their line, below which is a series of unbaited hooks. Attracted by this decoy, another ayu is foul-hooked as it comes out to defend its feeding territory.

Herbivory is, however, much more common in tropical freshwaters, where seasonal flooding inundates forests and plains. Here fishes such as the grass carp (*Ctenopharyngodon*) can feed on grasses, and decaying vegetation, while fruits, flowers, and seeds that fall into the water are seized by fishes such as the cyprinid *Puntius* or fruit and nut eating characins, including the tambaqui (*Colossoma macropomum*) which can attain a weight of 30 kg, and species of piranhas (*Serrasalmus*). As in phytoplankton feeders, filter-feeders, and mammalian herbivores, herbivorous fish have longer guts with greater surface area for absorption than carnivores or omnivores. As a rough rule, the ratio of gut length to body length is greater than 3 in herbivorous fishes, from 1 to 3 in omnivores and less than 1 in carnivores.

Unusual food types

Fish have also evolved adaptations that permit them to feed on the fins, scales, mucus, blood (lampreys, candiru (*Vandellia cirrhosa*), male angler fish), even the eyes (*Haplochromis compressiceps*) of other organisms. Such species typically possess highly specialized, often bizarre morphological and behavioral adaptations. Cleaner fish that feed on ectoparasites also provide interesting examples of symbiotic relationships between the small cleaner and the usually much larger host species as described in Chapter 13.

Envoi

Food and feeding presents some of the most interesting applications of current ecological theory and modern technology in the study of the lives of fishes. How fishes acquire their food, what they eat, and how that food is utilized are all fundamental questions facing investigators. Traditional studies, often based on stomach contents, are now enhanced by computer modeling, electromyographic recording, and digital photographic techniques that allow for real-time, *in-vivo* data collection on feeding habits.