gene pool; establishing the ecophysiological conditions that deliver this is still a challenge.

See also

Antarctic Fish. Deep-sea Fishes. Eels. Fish Larvae. Intertidal Fishes. Salmonids.

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FISH FARMING

See **MARICULTURE DISEASES AND HEALTH; MARICULTURE OF AQUARIUM FISHES; MARICULTURE OF MEDITERRANEAN SPECIES; MARICULTURE OVERVIEW; MARICULTURE, ENVIRONMENTAL, ECONOMIC AND SOCIAL IMPACTS OF**

FISH FEEDING AND FORAGING

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doi:10.1006/rwos.2001.0023

Introduction

There are approximately 24 600 species of fish of which 58% or 14 268 live in the sea. The sea covers about 71% of the surface area of the earth and has an average depth of around 3800 m, so that the total volume of the marine environment is about $1370 \times 10^6\,\mathrm{km}^3$. Much of this volume, removed from the influence of the sun's rays, is an inhospitable place to live, being dark, cold, and very low in available food. With such a volume for living, it is no surprise to learn that there are some 15 basic ways in which fish can gain food from the environment (**Table 1**). Because the open ocean and the deep ocean have low productivity compared with the shallow seas, most of the fish diversity is found in waters less than 200 m deep with the highest concentrations being found in tropical waters over coral reefs. The fish in these areas also have the greatest diversity of ways of making a living. Coral reefs and other inshore areas also have the most complex linking between fish with long food chains.

Modes of Feeding in Fishes

During the course of evolution, fish in the marine environment have developed a diverse array of behavioral, morphological, and physiological adaptations to cope with the food they most commonly eat. Although fish feeding habits can be classified into a relatively few groups, the diversity within each group is significant. The different modes of feeding are shown in **Table 1** together with a selection of illustrative species. With this table in mind, it becomes possible to examine in more detail the principles of behavioral adaptations used to cope with different conditions.

Feeding mode can be classified by the type of food eaten. A species adopting a particular type of food, say that of a piscivore, will develop a body form and a set of foraging tactics suiting it to the particular types of prey taken and the habitat in which the piscivore lives. For an example, a whiting

Table 1 Feeding modes of fishes: major trophic categories in fishes.

Category	*Examples*
1. Detritivore	Mullet, *Mugil*
2. Scavengers	Dogfish, *Squalus*; hagfishes, Myxinidae
3. Herbivores	
3.1 Grazers	Parrotfishes, Scaridae
3.2 Browsers	Surgeon fishes, Acanthuridae
3.3 Phytoplanktivores	Peruvian anchoveta, *Engraulis ringens*
4. Carnivores	
4.1 Benthivores	
(a) Picking at relatively small prey	Lemon sole, *Microstomus kitt*
(b) Disturbing then picking at prey	Gurnards, Triglidae
(c) Picking up substratum and sorting prey	Black surfperch, *Embiotica jacksoni*
(d) Grasping relatively large prey	Triggerfish, *Balistes fuscus*
4.2 Zooplanktivores	
(a) Filter feeders	Menhaden, *Brevoortia tynrannus*
(b) Particulate feeders	Anchovy, *Engraulis mordax*
4.3 Piscivores	
(a) Ambush hunters	Megrim, *Lepidorhombus wiff-iagonis*
(b) Lurers	Angler fish, *Lophius piscatorius*
(c) Stalkers	Trumpet fish, *Aulostomus maculatus*
(d) Chasers	Bluefin tuna, *Thunnus thunnus*

(*Merlangius merlangus*) living in shallow areas of the North Sea, uses vision to locate prey and has a larger mouth than an invertebrate feeder such as the haddock (*Melanogrammus aeglefinus*). The related rat-tail macrourid living at 3000 m depth is more likely to use olfaction or the lateral line to find prey and many deep-sea fish have very large mouths to allow them to take whatever prey they encounter. The categories in **Table 1** are a useful way to illustrate how form, function, and behavioral habits influence the characteristics of different feeding types.

Most shallow-water environments contain varying amounts of detritus derived from dead plants and animals. This can provide a source of food for some fish, although this mode does not comprise a major feeding type in the sea when compared with fresh waters. In **Table 1**, mullets (Mugilidae) are given as an example and this highlights a problem with the classification: the categories are not exclusive. Very few fish specialize to such a degree that they never eat anything but the prey type classed as their principal food. So, even though mullet species do eat detritus, they also graze on plant material and capture invertebrate food. It is probably true of all species that eat some detritus that this food source is a supplement to their diet, resorted to when other items are scarce.

A large range of fish types feed on the dead remains of other fish, marine mammals, or invertebrate species. Hagfish (Myxinidae) are primitive and have no jaws. Inside their buccal cavity they have teeth that are used to rasp flesh once they have attached themselves with the suckerlike mouth. Although they often feed on dead fish, they also consume living fish if they can first obtain a good hold on them. This is facilitated by the presence of an irregularity on the skin of the prey, such as a wound. Other species, such as the spur dog, *Squalus acanthias*, take dead material if it is available, although they mainly eat fish and larger invertebrates. As with many carnivores from other animal groups, dead meat is rarely ignored.

Herbivores in the sea are limited in their choice. They can either frequent the shallow waters and consume macroalgae or algae encrusting rocks, or they can live in the open water near the surface and eat phytoplankton. If they choose the second option, they are most likely also to eat zooplankton. Grazers and browsers are most common on coral reefs (**Table 2**), where there are numerous species feeding on algae. Many herbivores are very selective in the species they eat and the grazing effect has a strong influence on competition for space between algal species. Herbivorous fish on coral reefs adopt one of three feeding strategies: they defend a territory, with some species of damsel fish (Pomacentridae) 'tending' gardens; they can adopt a home range within which all feeding occurs, as exemplified by some species of pomacanthid angelfishes; or they feed in mixed species groups as in some surgeon fishes. Herbivores on a reef feed only during the day and hide in crevices during the night.

Although they are separated in **Table 1**, phytoplanktivores and zooplanktivores will be dealt with together. Fish that feed on plankton can adopt one of two tactics: either they can sieve the water to

Table 2 Proportions of different types of feeders in a temperate and a tropical marine system

Feeding category	*Gulf of Maine, Atlantic*		*Marshall Island, Pacific (coral reef)*	
	%	*N*	%	*N*
Herbivores				
Phytoplankton	0.7	1	0	0
Benthic diatoms	0	0	1.5	3
Filamentous algae	0	0	16.0	33
Vascular plants and seaweeds	0	0	8.7	18
Detritivores	0.7	1	3.9	8
Carnivores				
Zooplanktivores	16.9	25	6.3	13
Benthic invertebrates	41.2	61	54.9	113
Piscivores	39.2	58	[a]	
Omnivores	2.0	3	8.9	18

[a] Category absent.

extract the plankton or they can pick off items individually. The two are presented as individual tactics in **Table 1**, but in reality species will switch between the two depending on the density and size of food. For species focusing on phytoplankton, sieving is the only alternative, as the plants are too small to take individually. The Peruvian anchoveta (*Engraulis ringens*) takes a mixture of phytoplankton and zooplankton but, because phytoplankton is so rich, the bulk of what they eat could be of plant origin. Most other planktivores eat a mixture of both, with zooplankton predominating. The classic planktivores are species such as the herring (*Clupea harengus*), mackerel (*Scomber scombrus*), pilchard (*Sardina pilchardus*) and sprat (*Sprattus sprattus*). They live in the epipelagic region of the ocean, have fusiform streamlined bodies, and most often live in large shoals. Many of them make significant migrations to reach feeding areas that are seasonally worth exploiting. An example is the mackerel stock that spawns off south-west England in the spring and then migrates into the North Sea either via the west coast of Britain or up through the English Channel.

A wonderful example of a plankton feeder is the basking shark (*Cetorhinus maximus*). It is remarkable that such large animals, up to 10 m long, can be sustained by their microscopic prey. To survive, these 3000 kg fish have to filter very large volumes of water and do so by swimming for long periods with mouths wide open. Fine rakers on the gill arches act as filters removing plankton from the stream of water leaving the gill slits.

In planktivores such as the herring, prey items are mostly selected and the frequency of prey species found in the stomach is not the same as their frequency in the environment. A famous study of the diet of herring by Sir Alister Hardy, made in the early 1920s, showed how complex the feeding habits of a fish are. Like all species of teleost fish, herring grow throughout their lives, starting as microscopic larvae and finally reaching a size of around 30–40 cm. As revealed by Hardy, the diet of the fish changes dramatically as the fish increases in size, and the figure that Hardy produced to show this (**Figure 1**) has become a classic of the marine biology literature. As larvae, the herring feed on very small planktonic prey such as the early stages of copepods, larval molluscs, tintinnids, and dinoflagellates. At this stage of their lives, herring are as much food for other fish as they are predators themselves. With growth, the young herring can begin to take larger planktonic prey such as the copepods *Pseudocalanus*, *Temora*, and *Acartia*, common in inshore waters off the British Isles. Juvenile and adult herring feed extensively on *Calanus finmarchicus,* one of the most common copepods, euphausiids (krill), amphipods, and fish. By changing their diet through their life history, the herring are moving niche too, and this also has a spatial component as the young herring live in nursery areas close inshore.

Carnivorous fish come in a wide range of forms (**Table 1**). A basic division is between species that feed mainly on prey dwelling in or on the bottom and those that take prey from the water column.

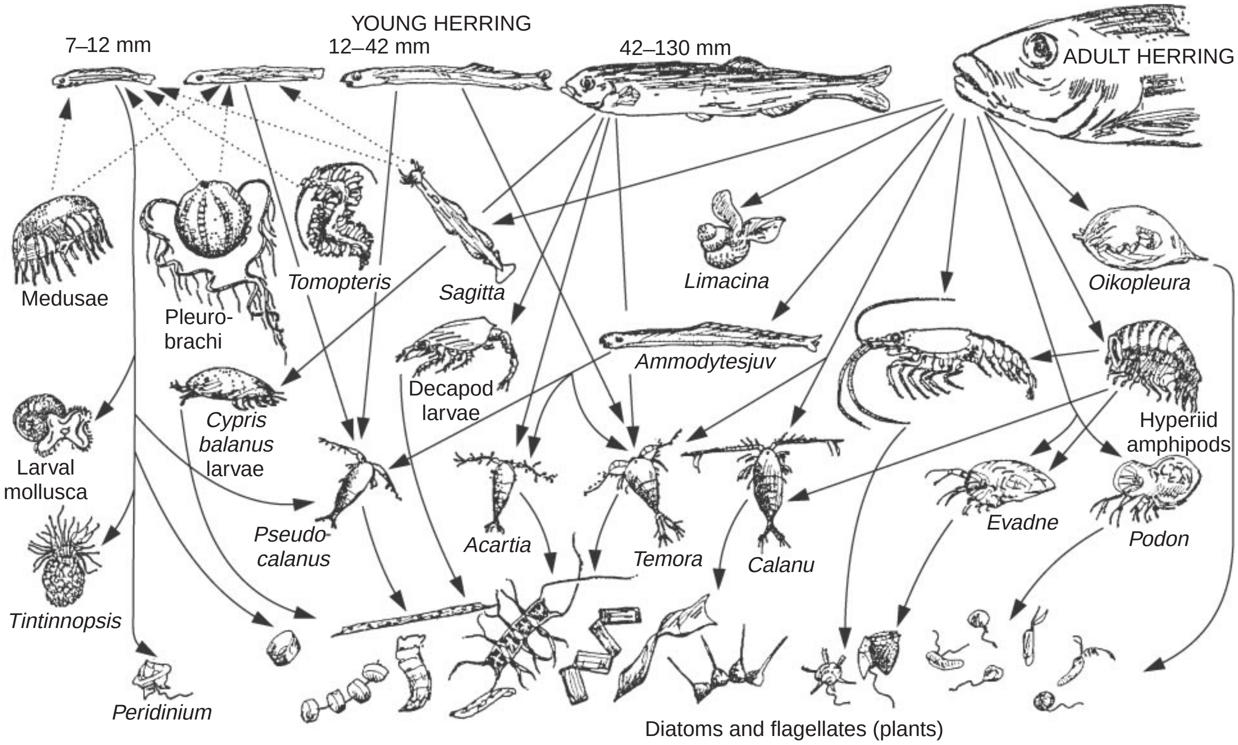

Figure 1 The food of herring from larval stages to adults. Also shown are the connections between the prey of herring and the food they eat. (Redrawn with permission from Hardy, 1924.)

Benthic feeding fish show a range of adaptations reflecting the differences in life style of the species. For example, the lemon sole (*Microstomus kitt*) is a visual feeder swimming over the bottom searching for annelid worms, which make up the bulk of its diet. In contrast, the sole (*Solea solea*) lies buried in the sand or mud during the day and forages only at night or when light conditions are very low during the day. It searches for food by touch. Both species could be categorized as 'benthivores' that pick at relatively small prey, but their differences are not insignificant. These differences are largely behavioral as both species are bottom dwellers superbly designed for their habitat, having flattened bodies and the habit of burying themselves in sediment.

As with herring, bottom feeders show life history changes in feeding behavior. For example, the black surf perch (*Embiotica jacksoni*), living on reefs off southern California, is named as an example in **Table 1** of a species that picks up substratum and, in the mouth, sorts prey from gravel and sand. These fish use this 'winnowing' tactic only once they have grown above a certain size. When they are small they fall into category 4.1a of **Table 1** as they feed by picking up each prey item. Their diet is limited, by the gape of the mouth, to food particles below a certain size.

The greatest problem for a piscivore is that its prey is mostly mobile and well able to see the predator coming. Two basic tactics are used by piscivores to capture prey; either they use stealth in various forms or they try to outswim the prey in a chase. These tactics have had profound influences on the selective forces influencing the fish found in each group. Those that use stealth have developed along two routes. Many species have special adaptations to lure prey close; the classic example of this is the angler fishes (Lophiidae) with their dorsal fin ray modified to form a movable rod with a lure on the end. These fish have also developed body coloration and shapes that camouflage them as they sit and wait on the bottom. Ambush hunters have used other means of getting close to prey. They hide in weed or adopt coloration that makes them inconspicuous. For example, the megrim (*Lepidorhombus wiff-iagonis*) eats mainly fish and shows the characteristic morphology of a piscivore despite its flattened body form. It has a slim body relative to other flatfish and has large eyes and mouth. To catch fish it lies half-buried on the bottom until a fish comes close, when it springs forward to make a capture.

Stalkers are also well camouflaged but get close to their prey by either using cover to disguise their intentions or by moving so slowly that the prey do not notice the advance until too late. For example, the trumpet fish (*Aulostomus maculatus*) living over coral reefs join shoals of nonpredatory fish as a way of coming close to their prey. The remarkable aspect of this tactic is that the trumpet fish changes its head color to match the color of the fish in the shoal.

Fish such as tuna (*Thunnus* spp.), the larger sailfish (*Istiophorous albicans*), and salmon (*Salmo salar*) at sea hunt their prey at speed. These fish have bodies designed for fast swimming and also have large mouths, often with backward pointing teeth, to grab the prey securely once caught. Many prey fish that are attacked in this way have developed behavioral tactics to reduce the risk of predation. They can shoal or school, they can develop camouflage, or they can avoid contact with predators by appearing only at night.

A few species of fish have specialized in exploiting others for food. At its most aggressive, this mode includes fish that eat scales or fins of other species, although most of the examples of these modes are from fresh water. Some species have adopted the role of cleaners who specialize in picking ectoparasites off other fish. This mode is not exploitative in that both sides of the interaction benefit. There are wrasse species (genus *Labroides*) in the Indo-Pacific that specialize entirely on cleaning and have a characteristic color scheme – blue with a longitudinal black stripe – that allows their 'clients' to identify them as cleaners. Any such system can be exploited: and the sabre-toothed blenny, *Aspridonotus taeniatus*, adopts the same color scheme as the labrids but when it gets close to the client it tears pieces of flesh out rather than picking off ectoparasites.

In describing the various modes of fish feeding we have seen that the success of individuals at capturing prey is a consequence of having the right morphology and behavior. It is also important to realize that many species are not confined to just one mode of feeding. The tactics adopted by a species can change with age or size, time of day, and geographical location. On a moment-to-moment basis the behavior adopted by a fish is critical in determining the diet taken and the energetic consequences of food intake. It is assumed in modern studies of foraging that behaviors have been molded by natural selection in the same way as has morphology.

Foraging Behavior

Given the assumption that behavior can be molded by natural selection, it becomes possible to analyze behaviors from an economic viewpoint. If a fish behaves so as to maximize its lifetime fitness then in the short term, it will choose to do things that maximize short-term gains such as increased growth rate or egg production and to minimize costs such as energy consumed or risk of predation during foraging. It then becomes possible to ask what behavioral strategy will maximize short-term gain or, in the jargon of foraging theory, optimize the behavior. With this approach it has been possible to predict what the optimal foraging strategy is for a species selecting prey from an environment with particular characteristics.

The way in which tunas behave while foraging near ocean fronts can be understood with the aid of optimality arguments. Tuna in the bluefin group (genus *Thunnus*) travel widely in search of prey. They have often been observed aggregating at ocean fronts where warm water is separated from cooler water by a narrow transitional zone. It is characteristic of these fronts that the productivity of tuna food is highest on the cool side of the front. This may be because the cooler water has recently upwelled and has higher plant nutrient levels. The dilemma facing the foraging tuna is that it prefers to be in the warmer water from a thermoregulation point of view but its best feeding opportunity is in the cooler water. Unlike many smaller fish, tuna have some control over their core body temperature. The vascular system has a heat exchange process by which blood moving from the center of the body outward passes vessels taking blood from the outside in. In this way the core temperature of a tuna can be maintained significantly above ambient and controlled at a relatively constant level. For the tuna this regulation becomes harder and more energetically costly in cool water, so that a prolonged stay in cool water could lead to death.

The question for the tuna then is to decide how long it should stay foraging in the cool water where food availability is higher than in the more 'comfortable' warm water on the other side of the front. Using optimality methods borrowed from engineering, it is possible to model the physiology and behavior of the fish and to calculate the energetic costs and benefits of the fish being in either the undesirable cold water with high food or the desirable warm water with low food. The model predicts that the fish will behave optimally, that is maximize its net energy gain, if it spends all of its nonfeeding time in the warm water, making quick sorties into the cold water area to fill its stomach. As soon as this has been achieved the fish withdraws again to the warm water to digest its meal. How long it has to stay in the cool water is a function of the abundance of food and the clarity of the water. The tuna is a visual predator, so the encounter rate with prey (prey met per unit time) will be a function of these two variables. Adopting this strategy will lead to the fish hovering around the boundary and, when applied to a school of tuna, may provide a mechanism for the observed aggregation behavior.

For many species, food acquisition takes place in a competitive environment. As already mentioned, some species shoal together in an attempt to reduce the individual risk of predation. One cost of this behavior is that all the individuals in the group will be searching in the same area for the same type of food, although group foraging often means that food is found faster. The optimal behavior for an individual will then depend on what others choose to do. Individuals cope with this type of competition in a number of different ways. Experiments with groups of cod (*Gadus morhua*) in large aquaria show that access to food items delivered one at a time is determined largely by the visual acuity, swimming speed, and hunger of each fish. The individuals that take the first few prey that are offered tend to be bigger than the others and hungrier, and may have a genetically determined basic higher metabolic rate. This type of competition by cod is usually termed scramble competition.

Other species handle group competition in different ways. For example, the omnivorous damsel fish, *Eupomacentrus planifrons*, defends a territory against conspecifics, so ensuring for itself a private supply of food. A further method of coping with intraspecific competition is to develop a hierarchy so that individuals can recognize the status of others from behavioral signals. When confronted with a dominant, a subdominant will give way without a fight. In this way the cost of contests is reduced, although the subdominant might be forced to feed as an opportunistic forager while the dominant takes a more selective diet. However, in the context of foraging in a group, the subdominant is doing the best it can.

If competing individuals are genetically related, or live together for a long time, individuals might be prepared to give way to a competitor in any particular interaction over food. In this way familiar or related competitors might operate on a tit-for-tat basis, so sharing the resource. There is some evidence from three-spined sticklebacks (*Gasterosteus aculeatus*) that this occurs. Fish that have been living together spend less time chasing a partner that has caught first a prey offered simultaneously to them both than do fish that have met for the first time in the competitive arena.

Situations in which the optimal behavior depends on how others behave are best handled theoretically using aspects of game theory. This predicts how rational decision makers should behave to maximize their payoffs in the face of competition. In fish behavioral studies aspects of game theory have been used to predict how groups of sticklebacks should divide themselves when exploiting patches of food with different profitabilities and how individuals of the same species should behave when two or more are approaching a predator to undertake what is called ‘predator inspection’. Here individual prey fish suddenly leave their shoal and swim deliberately toward a predator before turning back and rushing back to the safety of the shoal. Such individuals are often accompanied by one or more conspecifics that lag behind the leader. This behavior has been modeled as a cooperative interaction between the inspectors using a branch of game theory called the Prisoners’ Dilemma.

Food Chains

Everything that has been said so far emphasizes links between fish at various levels in the ecosystem, as shown in **Figure 1**. A similar diagram could be drawn for any species of fish, meaning that the dynamics of marine ecosystems is a function of the relationships established through feeding. Certain fish species have key roles to play in that they are prey for a wide range of species. One such species in the North Sea is the sand eel (*Ammodytes marinus*), which is a major food item for herring, mackerel, cod, whiting, pollack (*Pollachius pollachius*), saithe (*Pollachius virens*), haddock, bass (*Dicentrarchus labrax*), turbot (*Scophthalmus maximus*), brill (*S. rhombus*), megrim, plaice (*Pleuronectes platessa*), halibut (*Hippoglossus hippoglossus*), and sole. In addition, the sand eel is an important food item for many sea birds, particularly during the nesting season when, for example, the survival of puffin chicks (*Fratercula arctica*) depends on their parents bringing sufficient numbers of sand eels back to the nest.

This one example shows how critical the links between species are in a marine ecosystem. Early attempts at fisheries management in the North Sea, and in most other areas of the world, ignored the interconnectedness of species through trophic interactions. Since the late 1980s there has been an effort to take note of the interactions when fish stock assessment is carried out. One of the major effects of sustained fishing pressure on marine ecosystems has been the gradual reduction of abundance of the larger fish within a species and of the larger species. This has had the consequence of reducing the predation pressure on lower levels of the trophic web, so that species that have traditionally been given a low commercial value have increased in abundance and are all that is available. The sand eel illustrates this well. Until the early 1970s there was no significant fishery for sand eels in the North Sea. The growing demands for fish meal, generated by the poultry and pig production industries, created a market for previously unused species such as sand eels. Coupled with reduced catches of higher-valued species such as herring and cod, this stimulated fishermen to focus on sand eels and this, together with the continued sustained high levels of effort on the predators of sand eels is hastening the demise of the whole system. There have also been serious consequences for the sea bird populations that have suffered a number of years with little or no fledging of young.

See also

Benthic Organisms Overview. Coral Reef Fishes. Fisheries Overview. Fishery Management. Gelatinous Zooplankton. Large Marine Ecosystems. Mesopelagic Fishes. Pelagic Fishes. Plankton. Seabird Foraging Ecology. Upwelling Ecosystems.

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FISH HEARING, LATERAL LINES

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doi:10.1006/rwos.2001.0029

Introduction

Fishes, like other vertebrates, have a variety of different sensory systems for gathering information from the world around them. Each sensory system provides information about certain types of signals, and all of this information is used to inform the animal about its environment.

Although each of the sensory systems may have some overlap in providing information about a particular stimulus (e.g. an animal might see and hear a predator), one or another sensory system may be most appropriate to serve an animal in a particular environment or condition. Thus, for example, visual signals are most useful when a fish is close to the source of the signal, in daylight, and the water is clear. Chemical signals travel slowly in water and diffuse in haphazard directions, and so they are generally only effective over short distances. Acoustic signals have a unique advantage in that they travel very rapidly in water and are not interfered with by low light levels or murkiness of the water. Acoustic signals also travel great distances without decreasing in intensity, and this provides the potential for two animals that are some distance apart to communicate quickly.

Since sound is potentially such a good source of information, fishes have evolved several mechanisms to detect sounds, and many species use sound for communication between members of the same species. Indeed, it is very possible that the vertebrate ability to detect sound arose in fish ancestors in order for these animals to hear nonbiological as well as biological sounds in their environment. Thus, the most primitive vertebrates may have evolved hearing in order to detect sounds that are produced by waves breaking on the shore, water movement around reefs, or the swimming sounds produced by predators. It was probably only later in evolution that fish (and the later evolving terrestrial