

THE PHYSIOLOGY OF ANTIPREDATOR BEHAVIOUR: WHAT YOU DO WITH WHAT YOU'VE GOT

MARK ABRAHAMS

1. Introduction
2. The Probability of Death Once Detected by a Predator
 - 2.1. The Benefits of Being Small
 - 2.2. Avoidance at Close Range—The Mauthner System
3. Maximising the Probability of Detecting a Predator—The Detection Game
 - 3.1. Electrical
 - 3.2. Sound and Pressure
 - 3.3. Vision
 - 3.4. Chemical
 - 3.5. Sensory Compensation
4. Time Spent Vulnerable to Predation
 - 4.1. Temperature and the Abiotic Environment
 - 4.2. Hypoxic Environments
 - 4.3. Morphology
5. So What Do You Do With What You've Got?

1. INTRODUCTION

If you are a small fish, it is not an unreasonable assumption that you may potentially be eaten by any predator in whose mouth you fit (Figure 3.1). On the flip side, potential food for a small fish is usually restricted to that which fits in your mouth. By staying small you are limiting yourself to a restrictive subset of potential food items. With this very simplistic view of life as a small fish, it is possible to generate two rules for success:

1. Get big.
2. Do it fast.

If small fish conform to these rules, then I predict that being small is only a brief phase of a fish's life, and that ultimately all small fish, regardless of

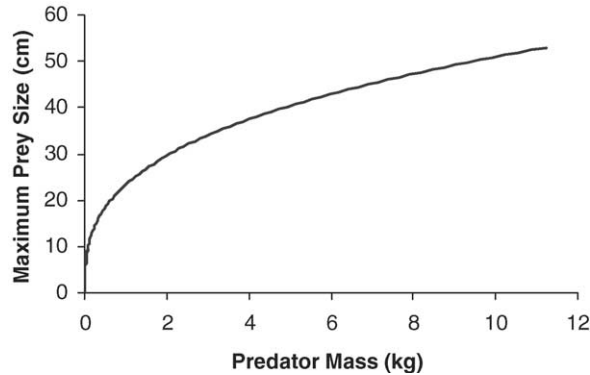


Fig. 3.1. The relation between the body mass of a brown trout predator (kg) and the maximum body length of Arctic charr prey (cm) it can consume. (Adapted from Nilsson, P. A., and Brönmark, C. (2000). Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos* **88**, 539–546, with permission from Blackwell Publishing.)

species, will seek to become as large as possible. You don't need to know a great deal about the diversity of different fish species to know that this prediction is wrong. Indeed, from an evolutionary perspective there is a trend for more derived species to be smaller than their ancestral form within North American fishes (Knouft and Page, 2003). A great many species never become large. And this is not due to some form of environmental constraint. Bringing these fish into captivity will not change the final outcome. These fish just remain small.

From the perspective of predator–prey interactions, it seems that a great many species just don't get it. They start small, grow at a relatively slow rate, and never achieve a very large final size. How come?

One potential explanation is that for many species, predation is just not a big deal. As a consequence, there may be little opportunity for selective predation by predators to impose such a phenotype on these species. A more pressing evolutionary force may be available habitat. Size of species is affected to a certain extent by the type of habitat, with smaller species tending to be found in smaller streams (Page and Burr, 1991). The vast majority of streams within North America are small (Leopold *et al.*, 1964), meaning that there is far more habitat available for small species (Knouft and Page, 2003). Another possibility is that these species really do want to become large, but are blocked by some sort of phylogenetic constraint. Or being small may not actually be that bad when dealing with predators. This Chapter will examine the latter argument.

In considering the role of physiology on antipredator behaviour, this Chapter considers the mechanisms as they relate to the three components that affect the probability of death from predation: the probability of being killed by a predator once detected, the probability of being detected by a predator, and the time spent vulnerable to predation (Lima and Dill, 1990).

2. THE PROBABILITY OF DEATH ONCE DETECTED BY A PREDATOR

2.1. The Benefits of Being Small

A popular tenet of many martial arts is to use the large size of your opponent to your own advantage. When you are a small fish being pursued by a much larger predator, there is a benefit associated with Newton's conservation of angular momentum. In simple terms, an object containing large mass (the predator) requires more energy to change direction than does an object containing less mass (the prey). This concept has been formalised in a mathematical theorem known as the Homicidal Chauffeur (Isaacs, 1965). This game posits the idea that you are trapped in a parking lot with a driver who is determined to kill you by running you down with their car and asks what are you going to do to provide yourself with the longest life expectancy (neither leaving the parking lot, phoning for assistance, nor acquiring some sort of military device are options).

The solution to the Homicidal Chauffeur is to veer perpendicular to the direction of motion of the car just before it gets close enough to strike you. The speed and mass of the car determine its minimum turning radius and so survival is determined by remaining within that turning radius. For a small fish trying to escape a predator, a single move of this sort may provide the opportunity for escape. This may come in the form of moving outside the detection range of the predator, finding a less vulnerable position within a group, or escaping into either a weed bed or rocky crevice.

Is there evidence that the Homicidal Chauffeur game is indeed a reasonable description of predator-prey interactions in fish? To adequately test this hypothesis, it is important to have good information about the angle at which the predator attacks the prey and the subsequent direction of escape by the prey, with the prediction that fleeing prey should delay their response to the last possible moment, and when they do they should flee in a direction perpendicular to that of the approaching predator. Although such research has not been addressed specifically with respect to this model, work has been done to investigate how the angle of escape is affected by the angle of approach by a predator. Webb and Skadsen (1980) found that minnows

were attacked by pike (*Esox lucius*) with a mean angle of 82 degrees. No data were presented on their “escape angle.” Domenici and Blake (1993) found that angelfish (*Pterophyllum eimekei*) have a preferential angular zone of escape between 130 and 180 degrees from a stimulus (sound emitted by two hydrophones). They argue such a response maximises the distance between the prey and an approaching predator and reflects subsequent changes of direction associated with the initial escape response (See also Domenici, 2002). Although the physics of predator–prey interactions are relatively simple, the underlying biology generates some complications.

In a recent paper, Odell *et al.* (2003) show that guppy (*Poecilia reticulata*) populations subject to a range of predator pressures exhibit corresponding changes in the physiology that underlies their ability to accelerate rapidly. They used second- and third-generation individuals that were derived from high and low predation regions within Trinidad. From these individuals, they obtained information on aerobic and burst swimming performance, morphological parameters (including an estimate of the swimming muscle mass), and enzymes associated with aerobic activity (citrate synthase), anaerobic activity (lactate dehydrogenase), and speed of muscle fiber contraction (myofibrillar ATPase). Their data demonstrated that the predation regime significantly increased the swimming muscle mass and lactate dehydrogenase activity, indicating the greater requirement for burst swimming performance in the presence of predators.

2.2. Avoidance at Close Range—The Mauthner System

When a predator is approaching rapidly and is very close, movement perpendicular to its direction may be a small fish’s only hope for survival. Virtually every species of fish contains a reflex response that makes a rapid, appropriate response possible. This has been demonstrated by Eaton and Emberley (1991) in which a negative relation exists for the angle of initial orientation for the prey fish and the angle of the escape turn. All this is made possible by the Mauthner system (Eaton *et al.*, 1997; Zottoli and Faber, 2000). The Mauthner system consists of two very large myelinated nerve fibers located on either side of the fish’s brainstem (Figure 3.2). These cells are connected to hair cells that are capable of detecting pressure waves on one side of the body, and then stimulating contraction of the muscles on the opposite side (Eaton *et al.*, 1997). In addition, once one cell has been stimulated, it acts to prevent the contralateral cell from responding. The net effect is to initiate a rapid response that should move the animal away from an approaching predator (Canfield and Rose, 1996). The response is also extremely rapid, with Mauthner cells firing within 3 to 4 ms of detecting the stimulus (Canfield and Rose, 1996). Contrast this with the human withdrawal response (i.e., the reflex that moves

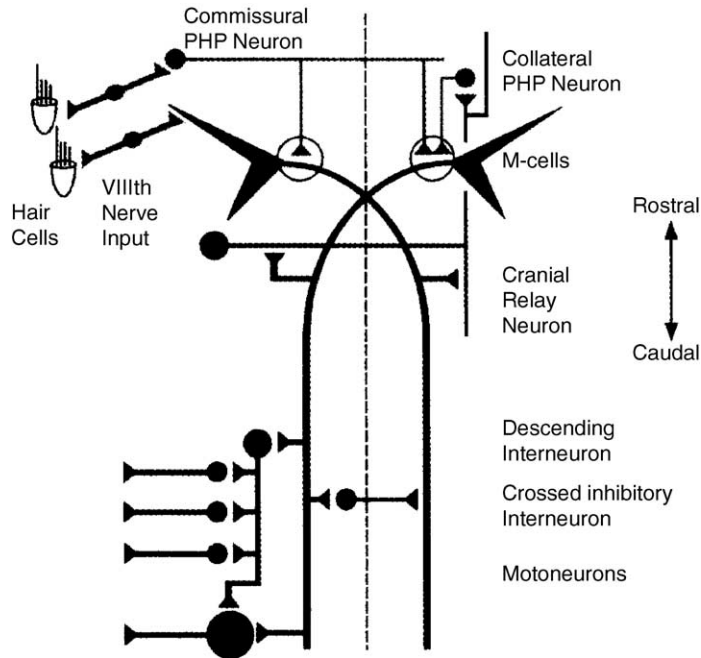


Fig. 3.2. Schematic illustration of Mauthner cells and their input and output neurons. Note that sensory neurons activate motoneurons on the side opposite stimulation and that the activated Mauthner cell inhibits the cell on the other side of the body. (Reprinted from Zottoli, S. J., and Faber, D. S. (2000). The Mauthner Cell: What has it taught us? *Neuroscientist* 6, 25–37, with permission from Sage Publications.)

your hand away from a hot surface), which takes 19 to 24 ms (Ganong, 2001). However, as seen below, the distance at which this reaction is likely to be initiated will probably be when the predator is very close to the prey and hence this reaction must be very fast. Some species are able to extend the range of detection of pressure waves by having sensory cells detect pressure changes within the swimbladder (Schellart, 1992). In essence, the Mauthner system represents the last chance that a prey has of escaping a predator.

3. MAXIMISING THE PROBABILITY OF DETECTING A PREDATOR—THE DETECTION GAME

Ideally, prey would rather not find themselves in a position where they are relying upon a very rapid reflex response to escape a predator that is now very close. Indeed, whoever detects who first may well determine the

outcome of a predator–prey interaction. It is important to note that should the prey detect the predator first, an immediate escape response is not always expected. Rather, the prevailing view among behavioural ecologists is that prey should make an adaptive response that weighs the benefits of remaining in its current location versus the costs of potentially being killed by a predator (Ydenberg and Dill, 1986). If the prey does detect the predator first, it may employ one of two options. The first is to communicate this information directly to the predator to allow both the prey and the predator to avoid a needless waste of energy (Hasson, 1991; Martin and López, 2001). This, of course, presents a conundrum because the prey must provide honest information to the predator that it has indeed been detected, such as precise information regarding its location. Although there are examples of such behaviour in fish (Sweatman, 1984), this does not seem to be the most prevalent system. The alternative is that once detected, small fish make an economic decision as to how close to allow the predator to approach prior to initiating their escape.

Most animals have no option but to incur some level of predation risk associated with most activities. As a consequence, it is reasonable to assume that both predator and prey are adapted to mutually detect and avoid each other. However, the mechanism of adaptation is constrained by variation in relative size. By definition, prey will be small and therefore present a smaller target to their predator. This may allow them to avoid detection until they get relatively close to a predator. In contrast, predators will be larger and therefore should have larger sensory apparatus that should increase the range at which prey are detected. From this perspective, predator–prey interactions are an information war. The weapon of choice will be dependent upon the dominant sensory modality.

Fish are capable of detecting their predators and prey using at least four different sensory modalities: electrical, sound (including pressure), chemical, and visual. This section will briefly discuss each sensory system with respect to predator–prey interactions, and then conclude with a discussion as to how fish may employ information from multiple sensory sources to make decisions associated with predator detection. For more detail on the sensory apparatus of fish, see Chapter 2.

3.1. Electrical

The ability of fishes to detect electrical information from within their environment was first described by Kalmijn (1966). To date, the ability to detect such information is limited to sharks, skates, and rays, as well as some catfishes, mormyrids, and Gymnotiformes. Two distinct mechanisms are known for using electrical information, passive and active detection. Passive

detection requires that the fish detect the electrical field that naturally exists around all organisms. These fields are generated by a variety of processes that include the underlying electrophysiology and hence the voltage differential that exists between organisms and their environment, streaming potentials generated as a consequence of water moving along an animal's skin, and the induced voltages that are generated as an organism moves through the earth's magnetic field (Kalmijn, 1988). Because such electrical fields decline in intensity with the cube of distance, the effective distance of such information is limited. Kajiura and Holland (2002) demonstrated that juvenile scalloped hammerhead sharks (*Sphyrna lewini*) ranging between 53 and 80 cm in total length have a detection range of up to 30 cm on either side of their head, or approximately one-half body length.

Employing a self-generated electrical field, electric fishes in South America (Gymnotiformes) and Africa (Mormyridae) can use an active electrical detection system. These groups are not closely related but are convergent in a number of characters, including their sensory abilities. This system detects other animals as they pass through and distort this electrical field. As with the passive system, the active form of detection also has a very short range. Nelson and MacIver (1999) measured maximum detection ranges for 14 to 18 cm long black ghost knifefish (*Apteronotus albifrons*) at 2 cm when foraging for the small invertebrate prey *Daphnia magna*. Given the very short detection range of both active and passive electroreception, it is unlikely they provide much benefit to potential prey in the form of early detection of predators.

3.2. Sound and Pressure

The physical properties of water are considerably different from air, meaning that pressure waves associated with either sound or the movement of an object have a relatively low attenuation rate, and hence a greater range than in air. Sound also moves four times faster in water than in air (Dusenbery, 1992), making it potentially a very important source of long-range information that may provide early warning of an approaching predator. Yet the qualities that may make this an important source of information may also be its downfall. Because of low attenuation rates, sound and pressure within water will contain a large amount of background noise that can potentially mask important information (Blaxter, 1988).

With respect to sound and pressure, a distinction is made between near- and far-field behaviour. Near-field behaviour is the pressure wave generated by an object moving through an incompressible medium such as water and is analogous to the bow wave generated by a moving boat. Generally, near-field waves have a lower frequency and tend to attenuate at shorter distances than do sound (far-field waves). Fish are capable of detecting low frequency

(i.e., 10 Hz) sound and pressure through the lateral line and inner ear sense organs at distances up to 100 m (Kalmijn, 1988). The lateral-line system also contains organs that are all oriented in different directions so that their combined response allows the orientation to the pressure wave to be determined (Coombs *et al.*, 1988). If an effective system exists for discriminating important information from background noise, the lateral line could provide effective early warning of an approaching predator, particularly for pelagic fish species.

The ability to detect sound and pressure is significantly enhanced by the presence of a swimbladder (Schellart, 1992). Due to differences in density, the swimbladder will vibrate more readily to environmental sound than other parts of the body, and this vibration can be transmitted to the ears by three specialised bones (the Weberian ossicles) in ostariophysans, anterior projections of the swimbladder in herrings, squirrelfish, and sciaenids, and connection via an auxiliary air bubble attached to the sacculle in mormyrids (Fritsch, 1999). Indeed, the swimbladder can be so important for hearing that some have speculated that the shape of the swimbladder is an adaptation that permits fish to detect the direction of sound (Barimo and Fine, 1998).

3.3. Vision

Within a predator–prey context, vision presents a very interesting paradox. As individuals become larger, so do their eyes. Larger eyes are better at gathering information from the environment. In a predator–prey context, this means a greater ability to detect potential predators and prey at greater distances. The paradox is that the larger eye, and hence larger size of an individual, then makes it visually more apparent to others that may be potential prey or predators.

The ability of the eye to provide visual information is quantified by visual acuity, which is the ability of the eye to resolve two points as separate objects. This is quantified by the following relation:

$$\frac{1}{\phi} = \frac{f}{s}$$

where ϕ is the angular separation of the individual receptors with its inverse being proportional to visual acuity, f is the focal distance within the eye, and s is the separation distance between retinal elements (Goldsmith, 1990). Because the focal distance within the eye is the distance between the lens and the retina, increasing this distance (and hence the size of the eye) will increase visual acuity. Reducing the separation distance (s) between visual receptors is constrained by a minimum size limit of 1 to 2 μm : receptors smaller than this size cannot function effectively as a light waveguide (Kirschfield, 1976;

Goldsmith, 1990). Because there appear to be limited options to manipulating s , it may be assumed that the only option to increase visual acuity ($1/\Phi$) is to increase f by increasing the size of the eye (Kiltie, 2000).

From the predator's perspective, the issue then is whether visual acuity, and hence the distance of detection, increases at a rate greater than the distance at which their increased size makes them apparent to their prey. To the author's knowledge, no such information currently exists and the reason may well be that a number of other factors will become important. The ability to detect an object will not solely be determined by visual acuity, but will also be affected by the characteristics of the target itself, specifically how it contrasts against the visual background. Most species are well designed to avoid detection by reducing their visual contrast, although there are exceptions. In particular, these would include species that are sexually dimorphic, with one species possessing colors that simultaneously advertise their presence to both potential mates and predators (Pocklington and Dill, 1995). Other physical characteristics of the environment, such as ambient light levels and the clarity of the water, will modify visual ability. Finally, the sensory abilities of both predator and prey may not be limited to the abilities of individuals alone. Fish in shoals are capable of using the senses of all individuals present, providing pooled information that increases their ability to detect any external stimuli (Godin *et al.*, 1988).

3.4. Chemical

To chemically detect a predator, it is important that there be a chemical reliably associated with a predator both in space and time. Although this seems obvious, it does impose some important conditions on the chemical. In particular, for fish that occupy relatively small bodies of water, the chemical must either rapidly degrade or diffuse to levels which are not detectable. This is critical because otherwise the correlation between the presence of the chemical and the likelihood of encountering a predator will diminish. With a low correlation, detection of the chemical will provide little or no useful information regarding the presence of predators and the risk associated with remaining within a particular habitat.

There is abundant literature that describes the chemical detection of predators (reviewed in Kats and Dill, 1998). The best known chemical for detecting predators or recent predation is alarm substance (AS) or Schreckstoffe (Smith, 1992). This chemical is possessed by fish within the superorder Osariophysi and is generally agreed to be hypoxanthine 3-N oxide (Pfeiffer *et al.*, 1985). The specific components that make this chemical biologically active have now been determined (Brown *et al.*, 2000, 2003). AS resides within the club cells of the epidermis of these fish and can only be

released when the fish has suffered physical damage that ruptures these cells (i.e., when it has been injured by an attacking predator). Fish that are capable of detecting AS often exhibit a fright reaction that can include a range of specific antipredator behaviours such as evasive swimming maneuvers, reduced motion, and movement to different habitats. In the field, AS will cause individuals to avoid the area for up to 12 hours after release (Mathis and Smith, 1992; Chivers and Smith, 1994). Other individuals will move into this location after only 3 hours, demonstrating that detection of the chemical cause fish to remember a location as being dangerous long after the chemical is no longer present in their environment (see also Chapter 1).

Fish need not only rely upon injured conspecifics to release this chemical. Some predators such as pike (*Esox lucius*) will release this chemical after they have consumed an Ostariophysid (Brown *et al.*, 1995a,b). The value of this chemical is not restricted only to species that produce this pheromone. Recent experiments have demonstrated that species that do not produce AS are capable of detecting and responding to this chemical, including some salmonids (Brown and Smith, 1998) and sticklebacks (Brown and Godin, 1997).

Crucian carp (*Carassius carassius*) are also able to chemically detect their predators, although their response to this information is not restricted only to antipredator behaviour. Petterson *et al.* (2000) have demonstrated that when carp detect the odor of a predator that has consumed prey containing AS, they respond by modifying their pattern of growth. In the presence of these cues, individuals from populations that contain predators will alter their pattern of growth so that they become deeper bodied. The importance of this tactic is discussed further in Section 4.3.

AS is not the only chemical known to generate antipredator behaviour. Some salmonids are also known to respond to the presence of the amino acid L-serine that is commonly found on the skin of mammals (Alderdice *et al.*, 1954; Idler *et al.*, 1956). When this chemical is detected, these fish will cease moving and feeding, and it is believed that such a response will then prevent their response to many types of gear associated with sport fishing. Such a response indicates that animals are capable of detecting and using any information that is reliable in signaling the presence of danger.

3.5. Sensory Compensation

Information within an ecosystem is now recognised as a valuable commodity, and one that organisms are prepared to pay for (Koops and Abrahams, 2003). This payment is usually in the form of sensory apparatus, such as their sensory neurons. Maintenance of these structures is expensive, and there is now evidence that varying environmental conditions can alter

investment in different sensory systems. Huber and Rylander (1992) examined eye size and the number of optic nerve fibers for six different species of minnows in the genera *Notropis* and *Cyprinella* in Texas and Oklahoma. They found that individuals that occupied turbid water had reduced eye size and as few as half the number of optic nerve fibers as those that occupied clear water. African cichlids also exhibit considerable variation in the extent to which their brains are developed for vision, olfaction, and mechanosensation (van Staaden *et al.*, 1995). In a review of the brain morphology of 189 species from Lakes Malawi, Tanganyika and Victoria, van Staaden *et al.* (1995) found that variation in light penetration within these lakes was the most important factor accounting for variation in visual and olfactory structures. Similarly, Brandstätter and Kotschal (1990) found a negative correlation of olfactory and visual abilities in cyprinid brains. Kotschal *et al.* (1998) have also found that cichlid species occupying locations with limited light penetration (e.g., turbid water or very deep locations) tended to invest more heavily in chemosenses and less so in visual detection. Schellart (1992) has reviewed the sensory capabilities of 63 marine and freshwater species and found that poor performance by one sense is usually compensated by enhanced abilities of other senses.

From this perspective, the evolutionary function of AS has been debated. Does it have as its primary function the role of communication (meaning that this chemical is a pheromone)? If so, have individuals evolved the ability to *produce* this chemical? Or does this chemical serve some other primary function, but individuals have evolved the ability to *detect* this chemical because its presence in the environment should be highly correlated with the presence of a predator?

If this chemical has evolved as a pheromone, then we must answer the evolutionary puzzle as to how such a system would evolve, because the only mechanism by which this pheromone can be released into the water is by an injury to the skin that ruptures the club cells. If this injury occurs from predation, the sender is likely in the jaws of a predator and therefore unlikely to benefit from this chemical. Two potential mechanisms have been proposed to provide a benefit to the sender. The first assumes that such individuals are likely in close contact with group members, and hence will receive a benefit either by increasing the survival of their kin or through reciprocal altruism that increases their own chance of survival (Smith, 1986). Another mechanism is that other predators are likely attracted by this chemical. These predators will then fight over the individual releasing this chemical, providing some finite chance of escape (Chivers *et al.*, 1996).

Such explanations have recently become suspect as fish apparently become less responsive to these chemical as the conditions of their environment approach natural conditions. Magurran *et al.* (1996) and Irving and

Magurran (1997) demonstrated that the response of European minnows to AS diminished within laboratory experiments as they added increasing structure to their environment. When these fish were placed in their natural environment, they exhibited no response to this chemical, leading them to conclude that fish may detect AS, but their response to this chemical depends upon context (but see Smith, 1997).

If AS is a signal, then individuals have the ability to detect it to obtain more information about the presence of predators. If this is the case, then there may be conditions under which individuals should react to this information and others where they will not. In contrast, if AS is a pheromone, individuals should react to its presence under all conditions. One simple explanation as to how such a system may operate is a sensory compensation model (Hartman and Abrahams, 2000). This model argues that individuals will react to some threshold concentration of AS, but the threshold concentration will be adjusted downwards (i.e., they will become more likely to react to AS) as fish perceive their environment to become more dangerous, and upwards as fish gain access to additional sources of information, such as vision (Figure 3.3). In laboratory experiments, Hartman and Abrahams (2000) manipulated risk of predation through the presence or absence of physical cover, or by altering the hunger levels of fish (hungry fish act as if

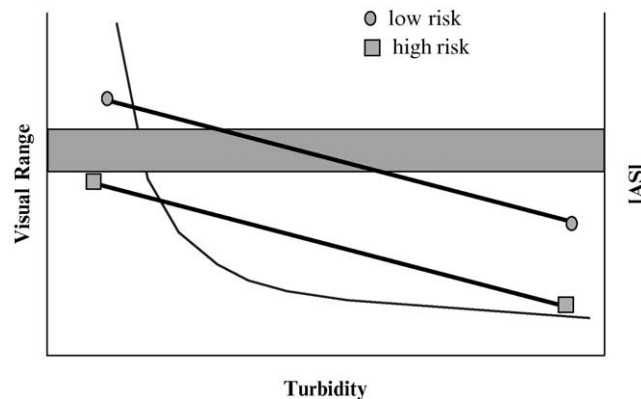


Fig. 3.3. The sensory compensation model. The grey bar indicates the concentration of alarm substance (AS) released. As indicated by the two parallel lines, the concentration of AS necessary to generate an antipredator response decreases as the level of predation risk increases. This threshold concentration also decreases in response to diminishing visual information due to increased turbidity. When faced with a high risk of predation, minnows should respond to a given concentration of AS in both clear and turbid water. With low risk, minnows should only respond to AS in turbid water. (Reprinted from Hartman, E. J., and Abrahams, M. V. (2000). Sensory compensation and the detection of predators: The interaction between chemical and visual information. *Proc. Roy. Soc. B* 267, 571–575, with permission from the Royal Society.)

they perceive their environment as being less dangerous). The value of visual information was manipulated by running the experiments in either clear or turbid water. Consistent with the model predictions, fish reacted to the introduction of AS under all high-risk conditions and when access to visual information was limited. However, increased access to visual information and reduced risk of predation consistently eliminated their response to AS. These data are consistent with the interpretation by Magurran *et al.* (1996) that AS is a cue, not a pheromone, and that fish combine information from multiple senses in assessing the level of predation risk associated with their habitat. This model further assumes that most freshwater species with well-developed eyes preferentially use visual information to assess the risk of predation because it will provide more detailed information about predator location, intent, and size (Chivers *et al.*, 2001).

Similar results have been observed by Smith and Belk (2001), in which they found that western mosquitofish (*Gambusia affinis*) rely primarily upon visual cues when engaging in various dangerous behaviours such as predator inspection, but use chemical and visual information additively for general avoidance behaviour. However, the relative importance of visual and chemical information in detecting predators is still being debated (see Wisenden and Thiel, 2002; Brown and Magnavacca, 2003; Wisenden *et al.*, 2004).

4. TIME SPENT VULNERABLE TO PREDATION

4.1. Temperature and the Abiotic Environment

Most fish are ectothermic, and hence their physiology is greatly influenced by their thermal environment. However, the response of most ectothermic fishes is not a simple consequence of how the ambient environment influences the rate of biochemical reactions but rather has an associated optimum (Huey and Kingsolver, 1989). From the prey's perspective, they should be seeking such an environment, but not necessarily if it happens to be the same environment that is also optimal for their ectothermic predators.

Within temperate ecosystems, not all fish have the same optimal temperature. Freshwater fishes of North America have been categorised into three general thermal preferences (cold-, cool-, and warm-water guilds), with these preferences approximating the different stratified and climatic thermal regimes (Magnuson and DeStasio, 1996). Curiously, not all physiological functions appear to have the same thermal optima, and as a consequence it has been argued that some fish have a daily vertical migration that allows them to take advantage of different thermal regions to maximise energetic intake (Wurtsbaugh and Neverman, 1988). This migration involves

fish moving from daytime, deep, cold regions to nighttime warm, shallow regions where they actively feed. It should be noted that a variety of different hypotheses have been posed to explain such shifts, including taking advantage of different light conditions that correlate with this vertical migration (see reviews by Lampert, 1989; Neilson and Perry, 1990). However, such a process does raise the intriguing possibility that use of shallow waters during the night or crepuscular periods may challenge visually-oriented predators.

It is known that the European minnow (*Phoxinus phoxinus*) and some salmonids become nocturnal at low water temperatures (Greenwood and Metcalfe, 1998). Although the reason for such a phenomenon is unknown, Greenwood and Metcalfe (1998) do speculate that many of these fishes' predators are diurnal endotherms. The low water temperature would therefore make them less able to escape attack and hence they become nocturnal to avoid exposure to such predators. Although this seems to be a reasonable explanation, there is no information that directly links temperature to predator-prey interactions in fish, but its impact is known for anurans. Anderson *et al.* (2001) found that increasing temperature was both a blessing and a burden for tadpoles. With increasing temperature, the tadpoles' growth rate increased. However, this growth had the associated cost of an increased mortality rate from predators. The underlying mechanism responsible for this result is not clear, although if movement rates are affected by temperature, this can generate such a result. Increased movement will increase encounter rates with both predators and prey (Werner and Anholt, 1993).

It is not unreasonable to assume a similar system operates for prey fish. As temperature increases, the energetic demands for fish will increase (Elliott, 1976). It is also known that increasing temperature will increase rates of movement for brown trout (*Salmo trutta*; Alanärä *et al.*, 2001). If both predator and prey are influenced in the same positive fashion by increasing temperature, then provided the temperature is neither becoming physiologically lethal nor significantly reducing dissolved oxygen levels (see below), the rate of predator-prey interactions should increase. However, changing temperature also generates an interesting caveat. Alanärä *et al.* (2001) have noted that the increased feeding rates will also increase rates of intraspecific competition such that individuals of lowest competitive ability may be unable to increase their feeding rate. Given that predators can be an important component in structuring an aquatic community (Werner *et al.*, 1983), those individuals unable to meet their increasing energetic demands may be the most likely to risk exposure to predators as a way to gain additional food (Abrahams and Cartar, 2000). However, it should be noted that even though gross rates of energetic intake can be achieved by feeding in

more dangerous locations (Abrahams and Dill, 1989), the net effect may be reduced because such locations can generate an increased metabolic cost through fear bradycardia (Cooke *et al.*, 2003).

Assuming that size will impact relative competitive abilities, Hughes and Grand (2000) have developed a model that predicts temperature-based size segregation between habitats. The relation between competitive ability and maximum ration size will determine whether smaller or larger fish preferentially occupy cooler waters. Currently there are no tests of this model, although these data are consistent with experimental work by Krause *et al.* (1998).

4.2. Hypoxic Environments

As long as there has been water, there has been considerable variation in the levels of dissolved oxygen. This can occur through variation in temperature or salinity that alters the solubility of different gasses in water (known as Henry's Law). Any body of water will also have processes that add and remove dissolved oxygen. These include agitation at the water's surface that allows atmospheric oxygen to dissolve into the water, and photosynthesis that produces oxygen. Respiration by any aerobic organism, including decomposition, will remove dissolved oxygen. As a consequence, aquatic ecosystems that have low light and reduced mixing such as heavily vegetated wetlands, flooded forests, and floodplain lakes will tend to have low levels of dissolved oxygen. Similarly, benthic regions of lakes, water subjected to extreme solar or geothermic heating, and the salinity gradients around estuaries will also be hypoxic. The consistent availability of hypoxic environments means that adaptation to such conditions has been a major evolutionary force affecting fish design. Such adaptations include increased gill ventilation rates, (Johansen, 1982; Randall, 1982; Smith and Jones, 1982), increased gill perfusion and consequent increase in functional gill surface area (Booth, 1979; Johansen, 1982), increased blood oxygen carrying capacity and affinity (Powers, 1980), and the behaviour and morphology necessary for aquatic surface respiration. Comparative studies indicate that chronic exposure to hypoxic conditions result in enlarged gill surface area (Hughes and Morgan, 1973; Palzenberger and Pohla, 1992; Chapman *et al.*, 1999, 2000, 2002; Chapman and Hulen, 2001; Schaack and Chapman, 2003) and the use of anaerobic metabolism (Blažka, 1958; Holeyton, 1980; Hochachka, 1986).

One mechanism by which fish can reduce aerobic metabolic pathways and activate anaerobic pathways is modification of lactate dehydrogenase isozyme distribution within major organs in response to long-term chronic hypoxia (Almeida-Val *et al.*, 1995). More recently, Almeida-Val *et al.* (2000)

analyzed the levels of lactate dehydrogenase and malate dehydrogenase within some of the major organs of one of the most hypoxia tolerant fish of the Amazon, *Astronotus ocellatus*. They found a positive relationship between hypoxia tolerance and body size, suggesting that the mechanism may be through the action of these enzymes increasing the anaerobic potential of these organs. But it is not clear whether the result from this species will apply generally to all fish species, because relationships between body size and the presence of these and related enzymes are not always observed (Somero and Childress, 1980; Pelletier *et al.*, 1993).

As individuals become larger, so too are they influenced by the forces that affect patterns of growth with increasing size (Schmidt-Nielson, 1984). A larger individual is not simply a scaled-up version of the smaller individual. Some parts of the body grow at rates different than other parts. One example is the negative allometric relationship for mass-specific gill-surface area (Muir, 1969; Hughes, 1984; Figure 3.4), suggesting that

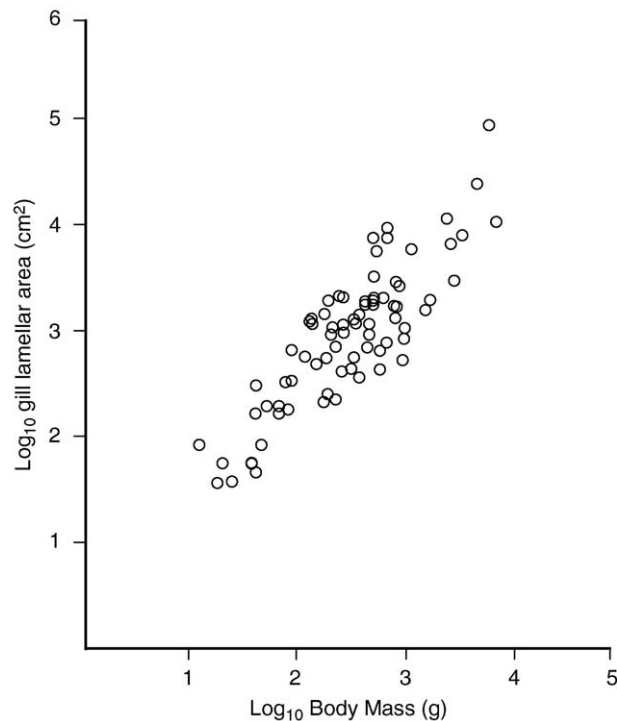


Fig. 3.4. The relation between log₁₀ gill lamellar area and log₁₀ body mass for several different fish species. (Reprinted from Muir, B. S. (1969). Gill dimensions as a function of fish size. *J. Fish. Res. Bd. Canada* **26**, 165–170, with permission from NRC Research Press.)

smaller individuals have more efficient gas exchange with their environment. Likewise, as individuals become larger, there is a well-known reduction in the respiratory rate per unit biomass (Schmidt-Nielson, 1984). When considering tolerance to hypoxic environments, a key component is whether factors that affect the rate of oxygen availability (i.e., gill surface-to-body volume ratios) are more than compensated by allometric scaling that reduces oxygen requirements.

A key parameter that may tip the balance in favor of the smaller fish is that respiratory rates can also be affected by fractal scaling. In its very simplest sense, allometric scaling relates to how two- and three-dimensional variables associated with areas and volume are affected as an animal becomes larger, measured in some one-dimensional parameter, usually either mass or length. Fractal scaling can describe how internal branching structures such as the circulatory system relate to animal size (West *et al.*, 1997, 1999). Given that the situation is significantly more complex, so too are the mathematics. However, there are really only two things that are important for this argument. First, for fractal scaling, there must be some component fundamental to the system under study that is relatively invariant as size changes. For gas transport, such a component is the red blood cell. The second is that the structure must somehow be a limiting factor affecting the physiology and survival of the organism in question. West *et al.* (1997, 1999) believe that because metabolic rates scale as three-quarters of the power of mass, and that such an exponent is inconsistent with allometric scaling, that the functional explanation associated with a fractal scaling model is the mechanistic argument from which this three-quarter power relationship is derived.

More recently, Darveau *et al.* (2002) have argued that metabolic rate is a complex process based upon many biological parameters, and that attempting to explain allometric scaling using a single parameter is folly. Their argument is compelling and may provide useful insight into understanding the processes that affect scaling relationships of metabolic rate. But hypoxia tolerance within fish may benefit from the approach advocated by West *et al.* (1997, 1999). A key distinction is that hypoxia tolerance represents an extreme challenge to the respiratory system and is determined by the physiological limits of the animal. As argued by Darveau *et al.* (2002), a problem with trying to develop a simple model to understand the scaling of basal metabolic rates is that they do not represent any physiological constraint, but reflect the combined energy requirements of all the cells within an organism. This rate can increase by many multiples to the maximum metabolic rate, which is dominated by the energy demand of the muscles, no longer all the cells of the body (Darveau *et al.*, 2002).

Regardless of the mechanism, there is evidence that small fish tend to be more tolerant of hypoxic environments than larger individuals. Robb and

Abrahams (2003) placed fathead minnows (*Pimephales promelas*) and their predator the yellow perch (*Perca flavescens*) in one of three different hypoxic environments. Within these hypoxic environments fathead minnows were capable of feeding and behaving normally for almost the entire duration of the three hour challenge, whereas yellow perch would lose equilibrium and have to be removed from the experiment after only 30 minutes (Figure 3.5). In addition, use of juvenile yellow perch that were the same size as the fathead minnows demonstrated an intermediate result that indicated that tolerance to hypoxia appears to be driven both by body size and species-specific parameters (Figure 3.5). Robb and Abrahams (2002) also demonstrated that fathead minnows were capable of visually detecting hypoxia stress in yellow perch at higher dissolved oxygen levels when these fish appeared outwardly healthy. These data suggest that if there is a size-based variation in hypoxia tolerance, then small fish may intentionally seek such locations to avoid attacks by their predators.

There is already some evidence in support of this hypothesis. Many lakes in temperate climates freeze over during the winter. When snow covers the

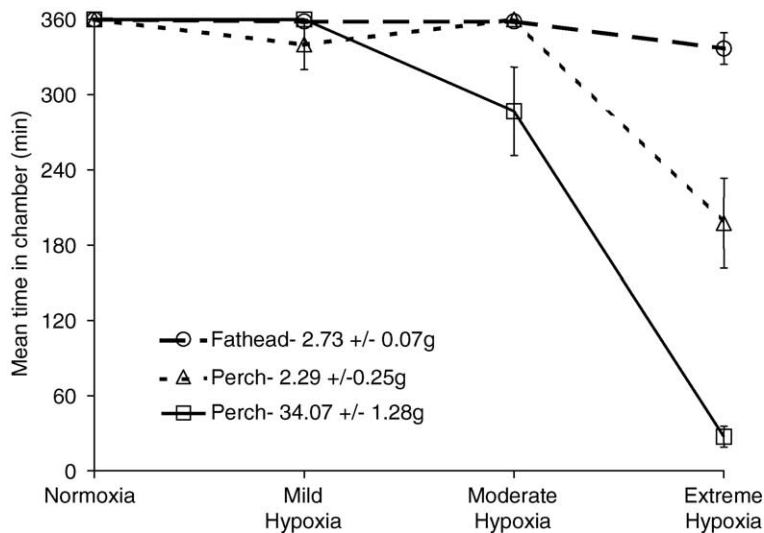


Fig. 3.5. The effect of variation in fish size and species on tolerance to a hypoxic environment. Fish were placed in an apparatus that had dissolved oxygen concentrations (measured in mg/l) of 7.2 (normoxic), 3.5 (mild hypoxic), 2.5 (hypoxic) and 1.8 (extreme hypoxic). Results measure the mean tolerance time (± 1 SE) spent in the chamber for all fish types (fathead minnow, small yellow perch or large yellow perch). (Reprinted from Robb, T., and Abrahams, M. V. (2003). Variation in tolerance to hypoxia in a predator and prey species: An ecological advantage to being small? *J. Fish Biol.* **62**, 1067–1081, with permission from Blackwell Publishing.)

ice, there is no longer any solar input into these lakes, stopping photosynthesis and hence the production of any additional dissolved oxygen to the lake. As a consequence, winter means a progressive decline in dissolved oxygen concentration. The longer the winter, the lower dissolved oxygen levels become. Klinger *et al.* (1982) and Fox and Keast (1990) have reported higher mortality of larger individuals within a species, suggesting that smaller individuals are more tolerant of hypoxic conditions. In Lake Victoria, the Nile Perch was introduced to provide a large species that could be harvested for food by fishers in the region. The Nile Perch did exceedingly well in this lake, consuming species within the highly diverse haplochromine assemblage and driving many species extinct. This change in the species composition of Lake Victoria fundamentally changed the lake's limnology. What was once a mesotrophic lake dominated by diatoms became a eutrophic lake dominated by blue-green algae (Hecky, 1993). Primary productivity doubled and ultimately the physical characteristics of the lake changed (Balirwa *et al.*, 2003). These included the development of hypolimnetic anoxia, almost year-round stratification of the deeper parts of the lake, and increasing hypoxia in shallower waters (Wanink *et al.*, 2001). Research by Chapman *et al.* (1996a,b, 1999) found that several species of haplochromines that were believed to be extinct were in fact extant within wetlands adjacent to the lake. These environments not only provide the structural complexity to assist fish in evading predators, but also contain hypoxic water that can not be tolerated by the Nile perch.

The most direct evidence of how hypoxic environments may affect predator-prey relationships comes from Rahel and Nutzman (1994). They captured mudminnows (*Umbra limi*) foraging for prey in the deep hypoxic waters of a bog lake. Restraining the mudminnows within the hypoxic regions in which they were feeding was lethal. This result indicates that the predatory mudminnows have modified their behaviour to allow them to forage in a lethal environment for short periods. Prey movement to this location does not provide a complete refuge from predators, but presumably the requirement to "dive" into this hypoxic region must constrain the predator's foraging ability.

Likewise, predatory fish may be able to take advantage of areas that have a horizontal distribution of hypoxic water. In particular, piscivorous fish that are capable of aquatic surface respiration will be able to enter such locations. The interesting caveat with such an approach is that the predators will be required to spend a considerable amount of their time near the surface of the water, rendering them particularly vulnerable to aerial predators (Kramer, 1987). Should such a situation exist within shallow hypoxic waters, then vulnerable prey species may effectively be protected by their predator's predators—a tritrophic predator refuge.

It should be noted that a variety of mechanisms will affect the ability of small fish to tolerate hypoxic environments and hence not every situation will fit the size-based model described above.

4.3. Morphology

Of more importance to prey are tactics to allow them to escape predation, and specifically to defeat predators by employing the most effective technique of all—not fitting in their mouth. Relationships between gape limitation (the biggest possible prey that can be consumed) and body size have been characterised for several species (Damsgård, 1995; Persson *et al.*, 1996; Nilsson and Brönmark, 2000; Magnhagen and Heibo, 2001; see Figure 3.1). What all of these studies tell us is that for a very large predator to be capable of consuming a prey that has increased its body depth, it must compensate by increasing its body mass as a cubic function of this change in length—or a considerable change in body mass is required to exploit larger size classes of prey. This relation has not been lost on prey species. Crucian carp are known to alter their pattern of growth when exposed to predators (Brönmark and Miner, 1992) and more recent experiments have shown that this altered growth is stimulated by chemical cues from predators that have consumed prey containing alarm substance (Pettersson *et al.*, 2000). Their response is to alter their normal allometric pattern of growth by becoming deep bodied and hence escaping predation by larger pike more rapidly than retaining their normal growth trajectory. The antipredator benefits of larger body size are amplified further when recognising that predators also have predators. The increased handling time associated with consuming larger prey can result in pike preferring prey smaller than would be predicted when considering only energetics (Nilsson and Brönmark, 1999). Because this is an inducible defense, there presumably must be some cost; otherwise, carp should adopt this morphology as a normal growth pattern. Pettersson and Brönmark (1999) theorised that this deep-bodied morphology must have a higher drag and therefore must be more energetically demanding when moving. Their laboratory experiments showed that this explanation was not quite that simple. Deep-bodied carp actually had a lower standard metabolic rate, and when moving at the velocity associated with the minimum cost of transport did not exhibit the increased energy consumption predicted from the increased drag hypothesis. However, when they increased their velocity there was a significant increase in energy requirements beyond what was observed for the normal morph, suggesting that they would fare poorly under intense intraspecific competition with the normal morph. This result provides a functional explanation for their earlier field experiments, in

which they demonstrated that the deep-bodied morph had an impaired ability to compete for food (Pettersson and Brönmark, 1997).

Changing overall body shape is not the only potential response to predators. Sticklebacks appear to develop lateral plates and armour in habitats that have greater densities of predators (Gross, 1978; Bell and Richkind, 1981). The combination of erect spines and lateral plates can render these fish immune to smaller predators, although this morphology may make them more vulnerable to invertebrate predators (Reimchen, 1980, 1983; Reist, 1980; Ziuganov and Zotin, 1995; Vamosi, 2002). Populations of *Galaxias platei* within Andean lakes also have a reduced caudal fin where they are associated with predators (Milano *et al.*, 2002). This morphology is hypothesised to make these fish more maneuverable and hence better able to escape attack by a predator. With this reduction in susceptibility to predation, these fish may then reap a competitive benefit when foraging for food in the presence of predators. The modification in behaviour in response to the risk of predation should be in proportion to the threat. If the threat is diminished by an altered morphology, these animals will not only enjoy reduced predation, but can also obtain a competitive advantage over other species that lack this morphological advantage (Grand, 2000; Abrahams, 1994, 1995). Antipredator morphology will allow these individuals to exploit the niche created by the risk of predation.

One additional option that prey have after encountering and successfully avoiding a predator is to hide within a refuge. Once within the refuge the prey is safe, but how long should prey stay there? Dill and Gillett (1991) provide an idea based upon economic theory, but the solution to this problem will be dependent upon the costs of remaining within a refuge. In particular, some species vary in their metabolic rates, meaning that the energetic costs associated with hiding are not equal for all species or individuals within a species. Krause *et al.* (2000) show that for two sympatric freshwater fishes, three-spine sticklebacks lose weight when in a nonfeeding refuge at a rate greater than do European minnow (*Phoxinus phoxinus*). They also observed that minnows tended to remain within a refuge for longer than the sticklebacks. They interpret this variation in refuge use as being consistent with the variation in cost associated with its use.

5. SO WHAT DO YOU DO WITH WHAT YOU'VE GOT?

There is an old joke about two field biologists who are preparing to work in a location that contains large numbers of grizzly bears. One biologist spots his colleague training on a local outdoor track. He asks why he's

training and the answer is that if they are attacked by a grizzly bear, he wants to be prepared. The first biologist scoffs, "That's ridiculous; you can't outrun a grizzly bear." To that his colleague responds, "I don't need to outrun the bear, I just need to outrun you."

The point of this story is that when examining what antipredator options are available, you must consider both the physiology of the animal and that of the other individuals and species that are likely to be subject to predation by the same predators. There has been considerable attention devoted to understanding which prey should be selected by predators to allow the predators to maximise their net rate of energy intake (see Stephens and Krebs, 1986). One specific component of this research is determining the characteristics of individual potential prey and whether they should or should not be included in a predator's diet. The detail of this theory is unnecessary here, but the main point is that three major components affect inclusion within a diet: the rate at which prey are encountered within the environment, the time it takes upon encounter to capture the prey, and the net energetic content of the prey. All that has been presented in this Chapter falls generally into these three categories. Prey physiology can influence their likelihood of encountering a predator by winning the detection war. Investment in sensory modalities will allow them to detect a predator before it detects them. If prey are able to do this, they will never be encountered and hence never consumed. This is unlikely to happen but also unnecessary. They need only win more of these detection games than other species within their environment. Likewise, unique features of a small fishes' physiology may allow them to occupy habitats that are inaccessible to their predators. Although such a situation likely has energetic costs, it does provide the ultimate opportunity to drive encounter rates with predators to zero.

However, prey cannot devote their entire lives to avoiding predation. If they did, they would be unable to gather resources, find mates, and pass this trait on to new generations. Rather, prey must ultimately risk exposure to predators to gain access to important resources, and they will have some finite encounter rate with predators. But even under these conditions, their physiology is partially designed to render them less preferred as a diet item. Some prey may contain potent toxins that render them poisonous to predators, or they may mimic such species to get off the menu (Gittleman and Harvey, 1980). However, even in the absence of this ultimate strategy, prey physiology possesses other tactics. These include the benefit of small size and increased maneuverability. This feature in conjunction with the Mauthner system means that predators that pursue their prey will often require considerable effort to capture them.

The validity of the "grow big and do it fast" rule can now be tested directly through hormonal and genetic manipulation of fish that elevates and

sustains growth hormone levels through all seasons (Devlin *et al.*, 1994; Du *et al.*, 1992). The impact of such manipulations upon the fishes' phenotypes has been profound and includes fish that can be up to ten times larger by 16 months of age and achieve sexual maturity in approximately one-half the time (Devlin *et al.*, 1995). The intriguing feature of genetically manipulated fish is that they are heterozygous for the transgene, meaning that a sib group will contain individuals that do and do not express this altered phenotype. Challenging genetically modified and wild-type Atlantic salmon with foraging decisions that involve a risk of predation also reveals a variation in behaviour that matches the variation in morphology. Size-matched individuals differ markedly in their willingness to risk exposure to a predator to gain access to additional food, whether this predator is restrained behind a transparent Plexiglas partition or if the fish must physically enter a location containing a predator (Abrahams and Sutterlin, 1999). Under both circumstances, salmon that have artificially elevated growth rates are much more willing to risk exposure to a predator and hence gain access to additional food.

Of course, to determine whether the modification in behavioural rules is associated with this altered growth pattern must ultimately involve a determination of whether the transgenic fish pay a much higher cost: are they more likely to be killed by predators under natural conditions? For obvious reasons, the simple experiment of releasing genetically modified salmon into the wild to assess their survival rates cannot be performed. To adequately understand the potential costs associated with transgenic manipulations, it is necessary to challenge these animals with environmental conditions that mirror those they will encounter in the field. This has now been done with newly hatched salmon and these data demonstrate that a mortality cost is associated with growth acceleration (Sundström *et al.*, 2004). Similar experiments have been attempted with transgenic smolts and so far have shown no mortality cost associated with the greater willingness of transgenic salmon to risk exposure to a predator (Abrahams and Devlin, unpublished data). However, challenging these larger-size classes of individuals with environmental conditions that mirror those they will face in the wild, while simultaneously meeting guidelines for the containment of genetically modified fish, make these experiments very difficult to perform. It is therefore not clear whether a failure to identify mortality costs for larger-size classes truly reflects less cost or an inability to adequately challenge these fish.

Almost all small fish species will have to confront some risk of predation associated with their evolutionary success. Whether feeding, finding a mate, obtaining and defending a spawning site or territory, or provisioning their young, there is some likelihood they will encounter a predator. The physiology of most small species is adapted to dealing with this problem, and not

simply by following the “grow fast and quickly” rule presented at the opening of this chapter. Their options are much more diverse and often benefit from the size difference between themselves and their predators.

ACKNOWLEDGEMENTS

I greatly appreciate the generosity of Geoff Eales, Ted Wiens, Robert MacArthur, Jennifer McLeese, and Kevin Campbell for lending an ear and providing advice on some of the topics discussed in this chapter. This chapter also benefited from the critical comments of Lauren Chapman, Gail Davoren, Larry Dill, Anne Magurran and one anonymous referee.

REFERENCES

- Abrahams, M. V. (1995). The interactions between antipredator behaviour and antipredator morphology: Experiments with fathead minnows and brook sticklebacks. *Can. J. Zool.* **73**, 2209–2215.
- Abrahams, M. V. (1994). Risk of predation and its influence on the relative competitive abilities of two species of freshwater fishes. *Can. J. Fish. Aquat. Sci.* **51**, 1629–1633.
- Abrahams, M. V., and Cartar, R. V. (2000). Within group variation in the willingness to risk exposure to a predator: The influence of species and size. *Oikos* **89**, 340–344.
- Abrahams, M. V., and Dill, L. M. (1989). A determination of the energetic equivalence of the risk of predation. *Ecology* **70**, 999–1007.
- Abrahams, M. V., and Sutterlin, A. (1999). The foraging and antipredator behaviour of growth enhanced transgenic Atlantic Salmon. *Anim. Behav.* **58**, 933–942.
- Alanärä, A., Burns, M. D., and Metcalfe, N. B. (2001). Intraspecific resource partitioning in brown trout: The temporal distribution of foraging is determined by rank. *J. Anim. Ecol.* **76**, 980–986.
- Alderdice, D. F., Brett, J. R., Idler, D. R., and Fagerlund, U. (1954). Further observations on olfactory perception in migrating adult coho and sping salmon: Properties of the repellent in mammalian skin. *Fish. Res. Bd. Canada* **98**, 10–12.
- Almeida-Val, V. M. F., Val, A. L., Duncan, W. P., Souza, F. C. A., Paula-Silva, M. N., and Land, S. (2000). Scaling effects on hypoxia tolerance in the Amazon fish *Astronotus ocellatus* (Perciformes: Cichlidae): Contribution of tissue enzyme levels. *Comp. Biochem. Phys. B* **125**, 219–226.
- Almeida-Val, V. M. F., Farias, I. P., Silva, M. N. P., Duncan, W. P., and Val, A. L. (1995). Biochemical adjustments to hypoxia by Amazon cichlids. *Braz. J. Med. Biol. Res.* **28**, 1257–1263.
- Anderson, M. T., Kiesecker, J. M., Chivers, D. P., and Blaustein, A. R. (2001). The direct and indirect effects of temperature on a predator-prey relationship. *Can. J. Zool.* **79**, 1834–1841.
- Bell, M. A., and Richkind, K. E. (1981). Clinal variation of lateral plates in threespine stickleback fish. *Am. Nat.* **117**, 113–132.
- Balirwa, J. S., Chapman, C. A., Chapman, L. J., Cowx, I. G., Geheb, K., Kaufman, L., Lowe-McConnell, R. H., Seehausen, O., Wanink, J. H., Welcomme, R. L., and Witte, F. (2003). Biodiversity and Fishery Sustainability in the Lake Victoria Basin: An Unexpected Marriage? *Bioscience* **53**, 703–715.
- Barimo, J. F., and Fine, M. L. (1998). Relationship of swim-bladder shape to the directionality pattern of underwater sound in the oyster toadfish. *Can. J. Zool.* **76**, 134–143.

- Blažka, P. (1958). The anaerobic metabolism of fish. *Phys. Zool.* **31**, 117–128.
- Blaxter, J. H. S. (1988). Sensory performance, behaviour, and ecology of fish. In “Sensory Biology of Aquatic Animals” (Atema, J., Fay, R. R., Popper, A. N., and Tavolga, W. N., Eds.), pp. 203–232. Springer-Verlag, New York.
- Booth, J. H. (1979). The effect of oxygen supply, epinephrine and acetylcholine on the distribution of blood flow in trout gills. *J. Exp. Biol.* **83**, 31–39.
- Brandstätter, R., and Kotrschal, K. (1990). Brain growth patterns in four European cyprinid fish species (Cyprinidae, Teleostei); roach (*Rutilus rutilus*), bream (*Abramis brama*), common carp (*Cyprinus carpio*) and sabre carp (*Pelecus cultratus*). *Brain Behav. Evol.* **35**, 195–211.
- Brönmark, C., and Miner, J. G. (1992). Predator-induced phenotypical change in body morphology in crucian carp. *Science* **258**, 1348–1350.
- Brown, G. E., Adrian, J. C., Jr., Naderi, N. T., Harvey, M. C., and Kelly, J. M. (2003). Nitrogen-oxides elicit antipredator responses in juvenile channel catfish, but not convict cichlids or rainbow trout: Conservation of the Ostariophysan alarm pheromone. *J. Chem. Ecol.* **29**, 1781–1796.
- Brown, G. E., and Magnavacca, G. (2003). Predator inspection behaviour in a characin fish: An interaction between chemical and visual information? *Ethology* **109**, 739–750.
- Brown, G. E., Adrian, J. C., Jr., Smyth, E., Leet, H., and Brennan, S. (2000). Ostariophysan alarm pheromones: Laboratory and field tests of the functional significance of nitrogen-oxides. *J. Chem. Ecol.* **26**, 139–154.
- Brown, G. E., and Godin, J.-G. J. (1997). Anti-predator responses to conspecific and hetero-specific skin extract by threespine sticklebacks: Alarm pheromones revisited. *Behaviour* **134**, 1123–1134.
- Brown, G. E., and Smith, R. J. F. (1998). Acquired predator recognition in juvenile rainbow trout (*Oncorhynchus mykiss*): Conditioning hatchery reared fish to recognise chemical cues of predator. *Can. J. Fish. Aquat. Sci.* **55**, 611–617.
- Brown, G. E., Chivers, D. P., and Smith, R. J. F. (1995a). Fathead minnows avoid conspecific and heterospecific alarm pheromones in the faeces of northern pike. *J. Fish Biol.* **47**, 387–393.
- Brown, G. E., Chivers, D. P., and Smith, R. J. F. (1995b). Localised defecation by pike: A response to labelling by cyprinid alarm pheromone? *Behav. Ecol. Sociobiol.* **36**, 105–110.
- Canfield, J. G., and Rose, G. J. (1996). Hierarchical sensory guidance of Mauthner-mediated escape responses in goldfish (*Carassius auratus*) and cichlids (*Haplochromis burtoni*). *Brain Behav. Evol.* **48**, 137–156.
- Chapman, L. J., Chapman, C. A., Nordlie, F. G., and Rosenberger, A. E. (2002). Physiological refugia: Swamps, hypoxia tolerance, and maintenance of fish biodiversity in the Lake Victoria Region. *Comp. Biochem. Phys.* **133(A)**, 421–437.
- Chapman, L. J., Chapman, C. A., Brazeau, D., McGlaughlin, B., and Jordan, M. (1999). Papyrus swamps and faunal diversification: Geographical variation among populations of the African cyprinid *Barbus neumayeri*. *J. Fish Biol.* **54**, 310–327.
- Chapman, L. J., Chapman, C. A., and Chandler, M. (1996a). Wetland ecotones as refugia for endangered fishes. *Biol. Conserv.* **78**, 263–270.
- Chapman, L. J., Chapman, C. A., Ogotu-Ohwayo, R., Chandler, M., Kaufman, L., and Keiter, A. E. (1996b). Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. *Cons. Biol.* **10**, 554–561.
- Chapman, L. J., Galis, F., and Shinn, J. (2000). Phenotypic plasticity and the possible role of genetic assimilation: Hypoxia-induced trade-offs in the morphological traits of an African cichlid. *Ecol. Lett.* **3**, 388–393.
- Chapman, L. J., and Hulen, K. (2001). Implications of hypoxia for the brain size and gill surface area of mormyrid fishes. *J. Zool.* **254**, 461–472.

- Chivers, D. P., Brown, G. E., and Smith, R. J. F. (1996). Evolution of chemical alarm signals: Attracting predators benefits alarm signal senders. *Am. Nat.* **148**, 649–659.
- Chivers, D. P., Mirza, R. S., Bryer, P. J., and Kiesecker, J. M. (2001). Threat-sensitive predator avoidance by slimy sculpins: Understanding the role of visual versus chemical information. *Can. J. Zool.* **79**, 867–873.
- Chivers, D. P., and Smith, R. J. F. (1994). Intra- and interspecific avoidance of areas marked with skin extract from brook sticklebacks (*Culaea inconstans*) in a natural habitat. *Env. Biol. Fishes* **49**, 89–96.
- Cooke, S. J., Steinmetz, J., Degner, J. F., Grant, E. C., and Philipp, D. P. (2003). Metabolic fright responses of different-sized largemouth bass (*Micropterus salmoides*) to two avian predators show variations in nonlethal energetic costs. *Can. J. Zool.* **81**, 699–709.
- Coombs, S., Janssen, J., and Webb, J. C. (1998). Diversity of lateral line systems: Evolutionary and functional considerations. In “Sensory Biology of Aquatic Animals” (Atema, J., Fay, R.R., Popper, A. N., and Tavolga, W. N., Eds.), pp. 553–594. Springer-Verlag, New York.
- Damsgård, B. (1995). Arctic charr, *Salvelinus alpinus* (L.), as prey for piscivorous fish: A model to predict prey vulnerabilities and prey size refuges. *Nord. J. Fresh. Res.* **71**, 190–196.
- Darveau, C.-A., Suarez, R. K., Andrews, R. D., and Hochachka, P. W. (2002). Allometric cascade as a unifying principle of body mass effects on metabolism. *Nature* **417**, 166–170.
- Devlin, R. H., Yesaki, T. Y., Donaldson, E. M., Du, S. J., and Hew, C.-L. (1995). Production of germline transgenic Pacific salmonids with dramatically increased growth performance. *Can. J. Fish. Aquat. Sci.* **52**, 1376–1384.
- Devlin, R. H., Yesaki, T. Y., Biagi, C. A., Donaldson, E. M., Swanson, P., and Chan, W.-K. (1994). Extraordinary salmon growth. *Nature* **371**, 209–210.
- Domenici, P. (2002). The visually mediated escape response in fish: Predicting prey responsiveness and the locomotor behaviour of predators and prey. *Mar. Fresh. Behav. Physiol.* **35**, 87–110.
- Domenici, P., and Blake, R. W. (1993). Escape trajectories in angelfish (*Pterophyllum eimekei*). *J. Exp. Biol.* **177**, 253–272.
- Dill, L. M., and Gillett, J. F. (1991). The economic logic of barnacle *Balanus glandula* (Darwin) hiding behaviour. *J. Exp. Mar. Biol. Ecol.* **153**, 115–127.
- Du, S. J., Gong, Z., Fletcher, G. L., Shears, M. A., King, M. J., Idler, D. R., and Hew, C.-L. (1992). Growth enhancement in transgenic Atlantic salmon by the use of an “all fish” chimeric growth hormone gene construct. *Biotechnology* **10**, 176–181.
- Dusenbery, D. B. (1992). “Sensory Ecology: How organisms acquire and respond to information.” W.H. Freeman and Co., New York.
- Eaton, R. C., and Emberley, D. S. (1991). How stimulus direction determines the trajectory angle of the Mauthner initiated escape response in a teleost fish. *J. Exp. Biol.* **161**, 469–487.
- Eaton, R. C., Guzik, A. L., and Casagrand, J. L. (1997). Mauthner system discrimination of stimulus direction from the acceleration and pressure components at sound onset. *Biol. Bull.* **192**, 146–149.
- Elliott, J. M. (1976). The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature, and ration size. *J. Anim. Ecol.* **45**, 923–948.
- Fox, M. G., and Keast, A. (1990). Effects of winterkill on population structure, body size and prey consumption patterns of pumpkinseed in isolated beaver ponds. *Can. J. Zool.* **68**, 2489–2498.
- Fritsch, B. (1999). Hearing in two worlds: Theoretical and actual adaptive changes of the aquatic and terrestrial ear for sound reception. In “Comparative Hearing: Fish and Amphibians” (Fay, R. R., and Popper, A. N., Eds.), pp. 15–42. Springer-Verlag, New York.
- Ganong, W. F. (2001). “Review of Medical Physiology” 20th ed., Lange Medical Books/McGraw-Hill Medical Publishing Division, New York.

- Gittleman, J. L., and Harvey, P. H. (1980). Why are distasteful prey not cryptic? *Nature* **286**, 149–150.
- Godin, J.-G.J., Classon, L. J., and Abrahams, M. V. (1988). Group vigilance and shoal size in a small characin fish. *Behaviour* **104**, 29–40.
- Goldsmith, T. H. (1990). Optimisation, constraint, and history in the evolution of eyes. *Quart. Rev. Biol.* **65**, 281–322.
- Grand, T. C. (2000). Risk-taking by threespine stickleback (*Gasterosteus aculeatus*) pelvic phenotypes: Does morphology predict behaviour? *Behaviour* **137**, 889–906.
- Greenwood, M. F. D., and Metcalfe, N. B. (1998). Minnows become nocturnal at low temperatures. *J. Fish Biol.* **53**, 25–32.
- Gross, H. P. (1978). Natural selection by predators on the defensive apparatus of the three-spined stickleback, *Gasterosteus aculeatus* L.. *Can. J. Zool.* **56**, 398–413.
- Hartman, E. J., and Abrahams, M. V. (2000). Sensory compensation and the detection of predators: The interaction between chemical and visual information. *Proc. Roy. Soc. B* **267**, 571–575.
- Hasson, O. (1991). Pursuit-deterrent signals: Communication between prey and predator. *TREE* **6**, 325–329.
- Hecky, R. E. (1993). The eutrophication of Lake Victoria. *Berhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **25**, 39–48.
- Hochachka, P. W. (1986). Defence strategies against hypoxia and hyperthermia. *Science* **231**, 234–241.
- Holeton, G. F. (1980). Oxygen as an environmental factor of fishes. In “Environmental Physiology of Fishes” (Ali, M. A., Ed.), pp. 7–32. Plenum, New York.
- Huber, R., and Rylander, M. K. (1992). Quantitative histological study of the optic nerve in species of minnows (Cyprinidae, Teleostei) inhabiting clear and turbid water. *Brain Behav. Evol.* **40**, 250–255.
- Huey, R. B., and Kingsolver, J. G. (1989). Evolution of thermal sensitivity of ectotherm performance. *TREE* **4**, 131–135.
- Hughes, G. M. (1984). Scaling of respiratory areas in relation to oxygen consumption of vertebrates. *Experientia* **40**, 519–652.
- Hughes, G. M., and Morgan, M. (1973). The structure of fish gills in relation to their respiratory function. *Biol. Rev.* **48**, 419–475.
- Hughes, N. F., and Grand, T. C. (2000). Physiological ecology meets the ideal free distribution: Predicting the distribution of size-structured fish populations across temperature gradients. *Env. Biol. Fishes* **59**, 285–298.
- Idler, J. R., Fagerlund, U. H. M., and Mayoh, H. (1956). Olfactory perception in migrating salmon. I. L-serine, a salmon repellent in mammalian skin. *J. Gen. Phys.* **39**, 889–892.
- Irving, P. W., and Magurran, A. E. (1997). Context-dependent fright reactions in captive European minnows: The importance of naturalness in laboratory experiments. *Anim. Behav.* **53**, 1193–1201.
- Isaacs, R. (1965). “Differential games: A mathematical theory with applications to warfare and pursuit, control and optimisation.” Wiley, New York.
- Johansen, K. (1982). Respiratory gas exchange of vertebrate gills. In “Gills” (Houlihan, D. F., Rankin, J. C., and Shuttleworth, T. J., Eds.), pp. 99–128. Cambridge University Press, Cambridge, MA.
- Kalmijn, A. J. (1988). Detection of weak electric fields. In “Sensory Biology of Aquatic Animals.” (Atema, J., Fay, R. R., Popper, A. N., and Tavolga, W. N., Eds.), pp. 151–186. Springer-Verlag, New York.
- Kalmijn, A. J. (1966). Electro-perception in sharks and rays. *Nature* **212**, 1232–1233.
- Kats, L. B., and Dill, L. M. (1998). The scent of death: Chemosensory assessment of predation risk by prey animals. *Ecoscience* **5**, 361–394.

- Kiltie, R. A. (2000). Scaling of visual acuity with body size in mammals and birds. *Funct. Ecol.* **14**, 226–234.
- Kirschfield, K. (1976). The resolution of lens and compound eyes. In “Neural Principles of Vision” (Zettler, F., and Weiler, R., Eds.), pp. 354–369. Springer-Verlag, Berlin.
- Klinger, S. A., Magnuson, J. J., and Gallepp, G. W. (1982). Survival mechanisms of the central mudminnow (*Umbra limi*), fathead minnow (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*) for low oxygen in winter. *Env. Biol. Fishes* **7**, 113–120.
- Knouft, J. H., and Page, L. M. (2003). The evolution of body size in extant groups of North American freshwater fishes: Speciation, size distributions, and Cope’s Rule. *Am. Nat.* **161**, 413–421.
- Koops, M. A., and Abrahams, M. V. (2003). Integrating the roles of information and - competitive ability on the spatial distribution of social foragers. *Am. Nat.* **161**, 586–600.
- Kotrschal, K., van Staaden, M. J., and Huber, R. (1998). Fish brains: Evolution and functional relationships. *Rev. Fish Biol. Fisheries* **8**, 373–408.
- Kramer, D. L. (1987). Dissolved oxygen and fish behaviour. *Env. Biol. Fishes* **18**, 81–90.
- Krause, J., Cheng, D. J.-S., Kirkman, E., and Ruxton, G. D. (2000). Species-specific patterns of refuge use in fish: The role of metabolic expenditure and body length. *Behaviour* **137**, 1113–1127.
- Krause, J., Staaks, G., and Mehner, T. (1998). Habitat choice in shoals of roach as a function of water temperature and feeding rate. *J. Fish Biol.* **53**, 377–386.
- Lampert, W. H. (1989). The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.* **3**, 21–27.
- Leopold, L. B., Wolman, M. G., and Miller, J. P. (1964). “Fluvial processes in geomorphology.” W. H. Freeman, San Francisco.
- Lima, S. L., and Dill, L. M. (1990). Behavioural decisions made under the risk of predation: A review and prospectus. *Can. J. Zool.* **68**, 619–640.
- Magnuson, J. J., and De Stasio, B. T. (1996). Thermal niche of fishes and global warming. In “Global Warming—Implications for Freshwater and Marine Fish” (Wood, C. M., and McDonald, D. G., Eds.), pp. 377–408. Society for Experimental Biology Seminar Series 61, Cambridge University Press, Cambridge, UK.
- Magnhagen, C., and Heibo, E. (2001). Gape size allometry in pike reflects variation between lakes in prey availability and relative body depth. *Funct. Ecol.* **15**, 754–762.
- Magurran, A. E., Irving, P. W., and Henderson, P. A. (1996). Is there a fish alarm pheromone? A wild study and critique. *Proc. Roy. Soc. London B* **263**, 1551–1556.
- Martin, J., and López, P. (2001). Are fleeing “noisy” lizards signalling to predators? *Acta Ethologica* **3**, 95–100.
- Mathis, A., and Smith, R. J. F. (1992). Avoidance of areas marked with a chemical alarm substance by fathead minnows (*Pimephales promelas*) in a natural habitat. *Can. J. Zool.* **70**, 1473–1476.
- Milano, D., Cussac, V. E., Macchi, P. J., Ruzzante, D. E., Alonso, M. F., Vigliano, P. H., and Denegri, M. A. (2002). Predator associated morphology in *Galaxias platei* in Patagonian lakes. *J. Fish Biol.* **61**, 138–156.
- Muir, B. S. (1969). Gill dimensions as a function of fish size. *J. Fish. Res. Bd. Canada* **26**, 165–170.
- Neilson, J. D., and Perry, R. I. (1990). Diel vertical migrations of marine fishes: An obligate or facultative process? *Adv. Mar. Biol.* **26**, 115–168.
- Nelson, M. E., and Mac Iver, M. A. (1999). Prey capture in the weakly electric fish *Apteronotus albifrons*: Sensory acquisition strategies and electrosensory consequences. *J. Exp. Biol.* **202**, 1195–1203.
- Nilsson, P. A., and Brönmark, C. (2000). Prey vulnerability to a gape-size limited predator: Behavioural and morphological impacts on northern pike piscivory. *Oikos* **88**, 539–546.

- Nilsson, P. A., and Brönmark, C. (1999). Foraging among cannibals and kleptoparasites: Effects of prey size on pike behaviour. *Behav. Ecol.* **10**, 557–566.
- Odell, J. P., Chappell, M. A., and Dickson, K. A. (2003). Morphological and enzymatic correlates of aerobic and burst swimming performance in different populations of Trinidadian guppies, *Poecilia reticulata*. *J. Exp. Biol.* **206**, 3707–3718.
- Page, L. M., and Burr, B. M. (1991). “A field guide to freshwater fishes: North America north of Mexico.” Houghton Mifflin, Boston.
- Persson, L., Andersson, J., Wahlström, E., and Eklov, P. (1996). Size-specific interactions in lake systems: Predator game limitation and prey growth rate and mortality. *Ecology* **77**, 900–911.
- Petterson, L. B., Nilsson, P. A., and Brönmark, C. (2000). Predator recognition and defence strategies in crucian carp, *Carassius carassius*. *Oikos* **88**, 200–212.
- Pfeiffer, W., Riegelbauer, G., Meier, G., and Scheibler, B. (1985). Effect of hypoxanthine-3-*N* oxide and hypoxanthine-1-*N*-oxide on central nervous excitation of the black tetra, *Gymnocorymbus ternetzi* (Characidae, Ostariophysi, Pisces) indicated by dorsal light response. *J. Chem. Ecol.* **11**, 507–523.
- Palzenberger, M., and Pohla, H. (1992). Gill surface area of water-breathing freshwater fish. *Rev. Fish. Biol. Fisheries*, **2**, 187–216.
- Pelletier, D., Guderley, H., and Dutil, J. D. (1993). Effects of growth rate, temperature, season, and body size on glycolytic enzyme activities in the white muscle of Atlantic Cod (*Gadus morhua*). *J. Exp. Zool.* **265**, 477–487.
- Pocklington, R., and Dill, L. M. (1995). Predation on females or males: Who pays for bright male traits? *Anim. Behav.* **49**, 1122–1124.
- Powers, D. A. (1980). Molecular ecology of teleost fish hemoglobins: Strategies for adapting to changing environments. *Am. Zool.* **20**, 139–162.
- Rahel, F. J., and Nutzman, J. W. (1994). Foraging in a lethal environment: Fish predation in hypoxic waters of a stratified lake. *Ecology* **75**, 1246–1253.
- Randall, D. (1982). The control of respiration and circulation in fish during exercise and hypoxia. *J. Exp. Biol.* **100**, 275–288.
- Reimchen, T. E. (1983). Structural relationships between spines and lateral plates in threespine stickleback (*Gasterosteus aculeatus*). *Evolution* **37**, 931–946.
- Reimchen, T. E. (1980). Spine deficiency and polymorphism in a population of *Gasterosteus aculeatus*: An adaptation to predators? *Can. J. Zool.* **68**, 1232–1244.
- Reist, J. (1980). Predation upon pelvic phenotypes of brook stickleback, *Culea inconstans*, by selected invertebrates. *Can. J. Zool.* **58**, 1253–1258.
- Robb, T., and Abrahams, M. V. (2003). Variation in tolerance to hypoxia in a predator and prey species: An ecological advantage to being small? *J. Fish Biol.* **62**, 1067–1081.
- Robb, T., and Abrahams, M. V. (2002). The influence of hypoxia on risk of predation and habitat choice by the fathead minnow, *Pimephales promelas*. *Behav. Ecol. Sociobiol.* **52**, 25–30.
- Schaack, S. R., and Chapman, L. J. (2003). Interdemic variation in the African cyprinid *Barbus neumayeri*: Correlations among hypoxia, morphology, and feeding performance. *Can. J. Zool.* **81**, 430–440.
- Schellart, N. A. M. (1992). Interactions between the auditory, the visual and the lateral line systems of teleosts; a mini-review of modelling sensory capabilities. *Neth. J. Zool.* **42**, 459–477.
- Schmidt-Nielson, K. (1984). “Scaling: Why is animal size so important?”. Cambridge University Press, New York.
- Smith, F. M., and Jones, D. R. (1982). The effect of changes in blood oxygen-carrying capacity on ventilation volume in the rainbow trout (*Salmo gairdneri*). *J. Exp. Biol.* **97**, 325–334.
- Smith, M. E., and Belk, M. C. (2001). Risk assessment in western mosquitofish (*Gambusia affinis*): Do multiple cues have additive effects? *Behav. Ecol. Sociobiol.* **51**, 101–107.

- Smith, R. J. F. (1997). Does one result trump all others? A response to Magurran, Irving, and Henderson. *Proc. Roy. Soc. London B* **264**, 445–450.
- Smith, R. J. F. (1992). Alarm signals in fishes. *Rev. Fish. Biol. Fisheries* **2**, 33–63.
- Smith, R. J. F. (1986). Evolution of alarm signals: Role of benefits of retaining group members or territorial neighbours. *Am. Nat.* **128**, 33–63.
- Somero, G. N., and Childress, J. J. (1980). A violation of the metabolism size scaling paradigm: Activities of glycolytic enzymes in muscle increase in large-size fish. *Phys. Zool.* **53**, 322–337.
- Stephens, D. W., and Krebs, J. R. (1986). “Foraging Theory.” Princeton University Press, Princeton, NJ.
- Sundström, L. F., Löhmus, M., Johnsson, J. I., and Devlin, R. H. (2004). Growth hormone transgenic salmon pay for growth potential with increased predation mortality. *Proc. Roy. Soc. Lond. B* **271**, S350–S352.
- Sweatman, H. P. A. (1984). A field study of the predatory behaviour and feeding rate of piscivorous coral reef fish, the lizardfish, *Synodus englemani*. *Copeia* **1984**, 187–194.
- van Staaden, M. J., Huber, R., Kaufman, L. S., and Liem, K. F. (1995). Brain evolution in cichlids of the African Great Lakes: Brain and body size, general patterns, and evolutionary trends. *Zoology* **98**, 165–178.
- Vamosi, S. (2002). Predation sharpens the adaptive peaks: Survival trade-offs in sympatric sticklebacks. *Ann. Zool. Fenn.* **39**, 1–28.
- Wanink, J. H., Kashindye, J. J., Goudswaard, P. C., and Witte, F. (2001). Dwelling at the oxycline: Does increased stratification provide a predation refugium for the Lake Victoria sardine *Rastrineobola argentea*? *Fresh. Biol.* **46**, 75–86.
- Webb, P. W., and Skadsen, J. M. (1980). Strike tactics of *Esox*. *Can. J. Zool.* **58**, 1462–1469.
- Werner, E. E., and Anholt, B. R. (1993). Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am. Nat.* **142**, 242–272.
- Werner, E. E., Mittelbach, G. G., Hall, D. J., and Gilliam, J. F. (1983). Experimental tests of optimal habitat use in fish: The role of relative habitat profitability. *Ecology* **64**, 1525–1539.
- West, G. B., Brown, J. H., and Enquist, B. J. (1999). The fourth dimension of life: Fractal geometry and allometric scaling of organisms. *Science* **284**, 1677–1679.
- West, G. B., Brown, J. H., and Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126.
- Wisenden, B. D., Vollbrecht, K. A., and Brown, J. L. (2004). Is there a fish alarm cue? Affirming evidence from a wild study. *Anim. Behav.* **67**, 59–67.
- Wisenden, B. D., and Thiel, T. A. (2002). Field verification of predator attraction to minnow alarm substance. *J. Chem. Ecol.* **28**, 433–438.
- Wurtsbaugh, W. A., and Neverman, D. (1988). Post-feeding thigmotaxis and daily vertical migration in a larval fish. *Nature* **333**, 846–848.
- Ydenberg, R. C., and Dill, L. M. (1986). The economics of fleeing from predators. *Adv. Study Behav.* **16**, 229–249.
- Ziuganov, V. V., and Zotin, A. A. (1995). Pelvic girdle polymorphism and reproductive barriers in the ninespine stickleback *Pungitius pungitius* (L.) from northwest Russia. *Behaviour* **132**, 1095–1105.
- Zottoli, S. J., and Faber, D. S. (2000). The Mauthner Cell: What has it taught us? *Neuroscientist* **6**, 25–37.