

Foraging behaviour in fishes: perspectives on variance

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Synopsis

The positive relationship between size of prey and frequency of ingestion by predators has been a focal point of investigations in foraging ecology. Field studies compare the frequency distribution of prey sizes in the predator's gut with that in the environment. Laboratory and field (enclosure) studies are based upon comparison of the frequency distributions of prey sizes in controlled environments, before and after the introduction of a predator. 'Optimal' caloric return for foraging effort (i.e. the theory of optimal foraging) has been widely used as a guiding principle in attempts to explain what a fish consumes. There is a body of information, however, which seems to indicate that the perceptual potentialities and cognitive abilities of a predator can account for both the direction of the prey size versus ingestion frequency relationship and the variance surrounding it. Part of this variance may be evidence of 'systematic ambiguity', a property of cognitive skills causing predators to respond to the same stimulus in different ways and to different stimuli in the same way. More extensive examination of cognitive skills (minimally defined as learning, remembering and forgetting) in fish may permit causal interpretations (immediate and ultimate) of variance in predatory skills. In such a paradigm of foraging behaviour, environmental stimulus is not taken as the predator's object of response (percept); a cognitive representation connects mind to stimulus and this is the criterion for the act of perception. Cognition, here considered as a formal system which acts upon representations, connects mind to response and thus to adaptation. Studies of the relationships among rates of learning, long and short-term memory, rates of forgetting, prey behavior, size and population turnover rates, lateralization of brain functions, diel fluctuations in predator activity levels and sleep, experience, and 'critical periods' in the development of the predator's nervous system should be examined in relation to foraging behaviour.

Introduction

Predators frequently select the largest manageable prey item available to them. Mean prey size increases with increasing predator size and with increasing predator-prey pursuit distance (Schoener 1979). Such patterns in predator-prey relations have been explained with theories of 'optimal foraging', which argue that predators should optimize

their energy (caloric) return per unit effort (Pyke et al. 1977, Krebs 1979, Schoener 1979). Optimal foraging is a subset of theories concerned with adaptive responses (strategies) in evolutionary biology. The principles of optimal foraging have been reviewed (Krebs 1979, Schoener 1979), tested (e.g. Diamond 1984) and critically evaluated (Cody 1974, Levins 1975a, b). Because every adaptive response becomes a factor in all subsequent adap-

tations, a multivariate approach to organism-environment relations (i.e. fitness) is necessary. Within such systems of interconnected adaptive traits, some traits may be at their selective optima while others are at their pessima. There is no need to assume that all adaptive responses are ultimately or immediately optimal (Levins 1975a, b). Accordingly, the nature and manner in which adaptive traits – e.g. perceptual abilities, cognitive skills and the ethological consequences of neurological development – are interconnected are proper, and perhaps essential, objects of study in trophic biology.

To focus attention on our subject we will consider the food size choice made by Atlantic salmon, *Salmo salar* alevins (Fig. 1). A clear positive trend, and some variance, is observed. If optimal foraging is invoked to explain these data, how are offlyers from this relationship to be explained; stochasticity alone? What is the biological basis of this foraging strategy? How does the predator determine the prey's caloric content? Is this ability hard-wired (genetically imprinted upon the animal's nervous system), learned, or some combination of the two? If learned, how rapidly? How is the learned response retained and for how long? How do these responses deteriorate when the prey population is

no longer abundant or when the predator grows and must pursue different prey? If a skill is hard-wired, how does it differ from perception per se (e.g. Brawn 1969, Maiorana 1981)? How does a hard-wired response remain selectively advantageous in a variable environment (e.g. short and long term climatic fluctuations)?

We introduce below the notions of perception, cognition and developmental neuroethology as substrates of foraging behaviour in juvenile fish. Our purpose is general, our literature review necessarily selective. We concentrate attention on the biology of Atlantic salmon, with which we are most familiar, but introduce salient insights from studies on other vertebrates in order to shed light on the meaning of patterns observed in the foraging behaviours of fish.

Feeding in Atlantic salmon alevins

Diurnal rhythms have been demonstrated in the feeding activity of juvenile fish (e.g. Oliphant 1957, Pinski 1967, Godin 1981). Browman & Marcotte (1986) have demonstrated diurnal rhythms in the intensity and skill with which Atlantic salmon alevins feed. Mean values of the fishes' total behavioural activity, feeding success and feeding error peaked at 0600–0900, 1100–1400 and 1900–2000 h. Variance (standard deviations around the mean) in total activity and feeding error was positively related to the mean. Mean frequency of ingestion peaked at 0600 h and declined asymptotically after 0800 h, although the total number of prey items in the fishes' gut remained unchanged throughout the day. The variance of ingestion frequency, however, followed the three peak trend of the other behavioural variables. The intensity of prey size selection generally increased during the day, with lows associated with periods of higher activity except in the evening. Selection of the largest prey (>0.8 mm) was associated with low light levels and high activity. These fluctuations in foraging behaviour and dietary selectivity appeared homologous to, and in almost perfect temporal agreement with, diurnal rhythms in wakefulness and sleep (which may be interpreted as levels

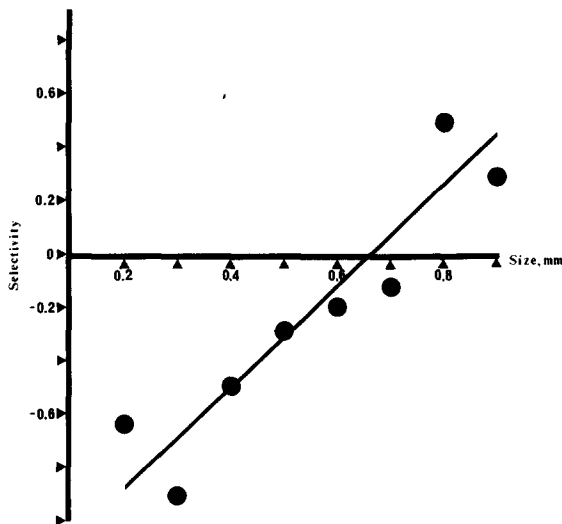


Fig. 1. Relationship between feeding electivity (Standardized Forage Ratio) and prey size for *Salmo salar* alevins. Line fitted by eye.

of cognitive/perceptual awareness) observed for other fish species (Fig. 2).

Feeding rates, capture success, ingestion rate and total activity in juvenile fish have been shown to change with the abundance of prey (Hunter 1980, Werner & Blaxter 1980, Sharp 1981, Morgan & Ritz 1984). Prey abundance affects the foraging behaviour of juvenile Atlantic salmon as well

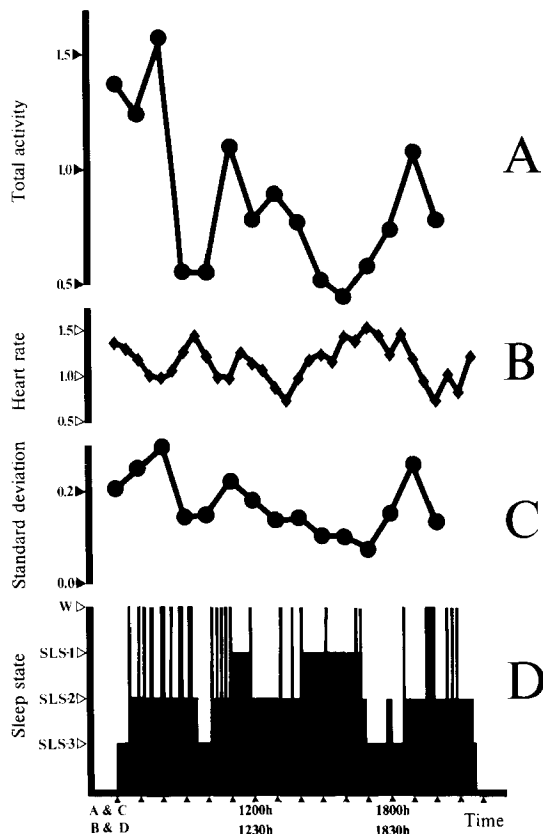


Fig. 2. A – *Salmo salar* alevins. The relationship between mean (for 10 fish) Total activity (#Eye fixations + #Moves + #Bites + #Misses + #Spits + #Social + #Ambiguous) per 3 min observation period (normalized for tank zooplankton abundance) and time of day (from Browman & Marcotte 1986). B – Diurnal periodicity in the heart rate of the catfish. Ordinate = time interval (seconds) between two subsequent heartbeats (redrawn from Karmanova et al. 1981). C – Variance in Total activity (Fig. 9A) as represented by its standard deviation. D – Diurnal periodicity in the wakefulness-primary sleep cycle of the catfish. SLS = sleep-like-state; SLS-1 = characterized by immobility with plastic muscle tone; SLS-2 = characterized by immobility with rigid muscle tone; SLS-3 = characterized by immobility with muscle relaxation; W = wakefulness (redrawn from Karmanova et al. 1981).

(Browman 1985). Above prey densities of 400 items per litre, 'sensory overload' led to optic tetanus (nystagmus, or uncontrolled repetition of ocular fixations) and caused success to decline (Fig. 3). The total number of prey items in the fishes' guts also followed this bell-shaped response pattern. There was some suggestion that selectivity of prey sizes was negatively affected by increased prey abundance, perhaps as a result of perceptual confusion (see below).

Background contrast affected the colour of prey selected by Atlantic salmon alevins (Browman 1985). Red prey were preferred under blue background conditions, blue prey against aqua-green backgrounds and unstained prey against red backgrounds. These studies clearly indicate the importance of controlling for time of day, prey density, and prey and background contrast in fish feeding experiments.

Perception as a source of variance in fish foraging behaviour

The perceptual abilities/limitations of fish necessarily affect their foraging behaviour (see, for ex-

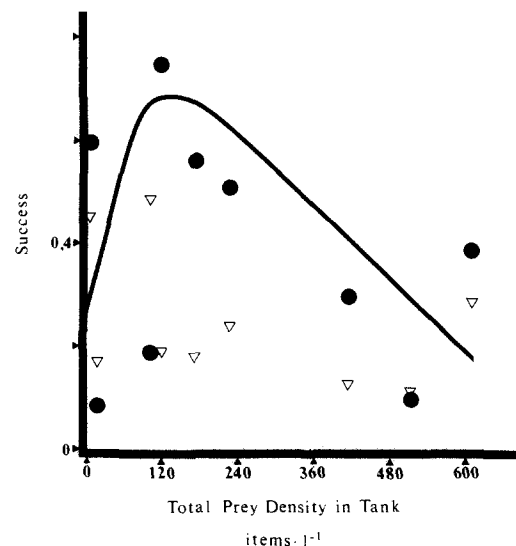


Fig. 3. *Salmo salar* alevins. The relationship between mean (for 10 fish) feeding success (#Ingestions/#Bites) and tank zooplankton density. Triangles are standard deviations around the means. Curve fitted by eye.

ample Dill 1983, Ringler 1983). It is to this aspect of fish biology that we now address ourselves.

Vision in fish is sensitive to differential prey movements against a kinematic background (e.g. Bateson 1889, Ingle 1968). Object orientation and direction of movement, form, texture and colour are also important in visual prey detection (e.g. Cronley-Dillon 1964, Jacobson & Gaze 1964, Sutherland 1968, Trevarthen 1968). In addition, the perceptual field of a fish's retina can be limited by environmental (or experiential) restrictions (or deprivations) during early development (Blaxter 1970, Ahlbert 1976). It is important, therefore, to control for these variables when considering trends in food selectivity by fish. It is possible that fish perceive the choreographies and second derivatives (i.e. accelerations and decelerations) of prey motion and not their size or taxonomic identity *per se* (Marcotte 1983).

Abundant prey may confuse fish predators (e.g. Williams 1964, Neill & Cullen 1974). Because large prey occur infrequently in most ecosystems, fish may minimize this confusion at intermediate prey densities by concentrating their attention on rare items. Thus, it is possible that fish 'select' large prey at intermediate densities for perceptual reasons, and not necessarily to optimize energetic returns. At very high densities (rare occurrences in natural environments, but the norm in hatchery settings), optic tetanus may render the animal incapable of making foraging decisions and dietary selection may tend toward randomness.

When humans observe two identical objects placed in the 'foreground' and 'background' of a flat polar projection (or other background which indicates a distant horizon) the object in the 'background' appears larger. This optical illusion applies until the image of the object subtends less than one degree of arc on the retina, at which point the reality of identity is perceived (Kaufman & Rock 1962, Ross *et al.* 1980). Juvenile fish have eyes on which, for any given object, a greater arc of retinal surface is subtended than for older, larger fish (Hairston *et al.* 1982). If this optical illusion occurs in fish, juveniles may be victimized more often than their older counterparts. As a consequence, a juvenile's prey size selection will be more variable and

less intense. Further, tests of the 'apparent prey size hypothesis' (e.g. Luecke & O'Brien 1981) which have used background polar projections to allow observers to estimate prey distances, may have inadvertently created this optical illusion. Given the similarity of vertebrate visual systems (see Ali 1975, Northmore *et al.* 1978), there is no strong reason to neglect such an idea as impossible or even unlikely for fish.

Images falling on the retina must flicker to be perceived (Cohen 1969). Flicker may be generated by the perceiver's motion (e.g. eye tremor) or may be environmentally induced, e.g. prey movement or wave generated flicker (McFarland & Loew 1983). Turbidity in water decreases the distance a predator can see, increases luminosity, decreases contrast, defocuses and dissipates wave generated flicker and changes the wave lengths of light transmitted through water (Marcotte, unpublished). All of these changes will affect a predator's ability to see distant prey, judge pursuit distances, and determine prey size, shape and colour. Previous studies have also indicated the need to control for effects of turbidity and the amount and kind of environmental lighting in experiments of foraging behaviour (e.g. Vinyard & O'Brien 1976, O'Brien 1979).

Cognition as a source of variance in fish foraging behaviour

Once a fish's perceptual abilities/limitations have been accounted for, cognitive skills can be considered to enable further explanation of trends and variance in dietary selections. For our purposes here, cognition can be minimally defined as learning, remembering and forgetting.

Cognition is to perception what syntax is to semantics (see Marcotte 1983); it is that mental function through which the organism creates mental representations of real stimuli, such as prey items. These representations possess attributes to which the organism responds – animals do not necessarily respond to external stimuli *per se*. For this reason, an animal can respond to the same stimuli in different ways, and to different stimuli in the same way. The result could be a systematic ambiguity in

observed behaviour which may be mistaken for stochastic variance in experimental examinations of food selection. Perception connects mind to stimulus; cognition connects mind to action. Perception is on the cutting edge of selection pressure; cognition is on the cutting edge of adaptation. Organisms do not adapt to an environment, they define it through mental representations and cannot adapt to an unperceived or unrepresented cause.

Two cognitive variables can be considered in the context of foraging behaviour and dietary selectivity, learning and memory: (1) Learning ability in fish has been adequately demonstrated (e.g. Ware 1971) and so we must ask: how fast does a fish learn appropriate responses to evasive prey and how does this change ontogenetically? (2) How does a fish remember learned responses? What are the durations of long and short-term memory (see Peeke et al. 1972), with and without reinforcements at various temporal frequencies. How do these durations change with development? Phrased differently; what is the turnover rate of 'search images' and how is this turnover related to development – especially given the continuous growth of the nervous system in fish (e.g. Johns & Easter 1975, Easter et al. 1977).

Learning is critical for juvenile fish. Hatchery-reared salmon do not feed as effectively upon release as do their wild counterparts and it may take up to two months for fish reared on artificial hatchery food to learn how to feed successfully on living prey (MacCrimmon 1954, Fenderson et al. 1968, Blaxter 1970, 1975, Sosiak et al. 1979, Shustov et al. 1980, Dickson & MacCrimmon 1982). Congruence, or lack of it, between developmental changes in the speed with which fish learn and forget (the dynamics of their memories) and the life histories and ecologies of available prey probably affect diet. The internal ecology of the predator must keep pace with that of its surroundings. For example, small prey are characterized by high reproductive potentials, short generation times and therefore high turnover frequencies and often short durations of population maxima (Fig. 4). Visual predators which feed on small prey must either feed non-selectively (e.g. filter feed) or must have the capacity to learn and forget 'search images'

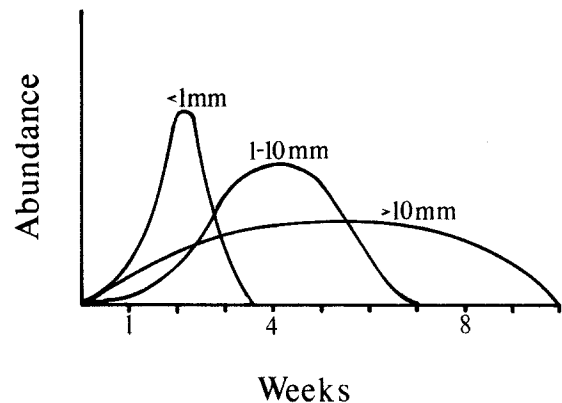


Fig. 4. Schematic representation of generational durations for hypothetical prey of three different sizes.

quickly (e.g. daily) to keep pace with the prey's turnover rate.

Developmental neuroethology and fish foraging behaviour

How learned responses can be made to resemble hard-wired stimulus-response arcs may hold a key to the developmental neuroethology of fish. Larval fish 'practice' feeding (e.g. Fortier 1983), implying that the 'critical period' for the development of learned skills and associated parts of the nervous system may be during the late embryonic and/or early larval periods. During these developmental intervals visual stimuli enter the fish's brain and comprehension (leading to learning) and response determination may be handled in a locus separate from that of the primary visual-motor center (Fig. 5). An effective response pathway may be selected in the motor nerve routes (e.g. trigeminal nerve), perhaps by neuronal competition (sensu Edelman & Finkel 1985). The dendritic arborizations of nerves in these selected pathways may become reduced and the axons may subsequently become myelinated. Later, the centres for comprehension, having executed their neuronal selection function, may divest themselves of memory functions as the visual-motor pathway is short-circuited (Fig. 5) and a true stimulus-response arc (Fig. 5B) is established (see also Luria 1978, Marcotte 1983). A behavioural suite, controlled by some established (selected)

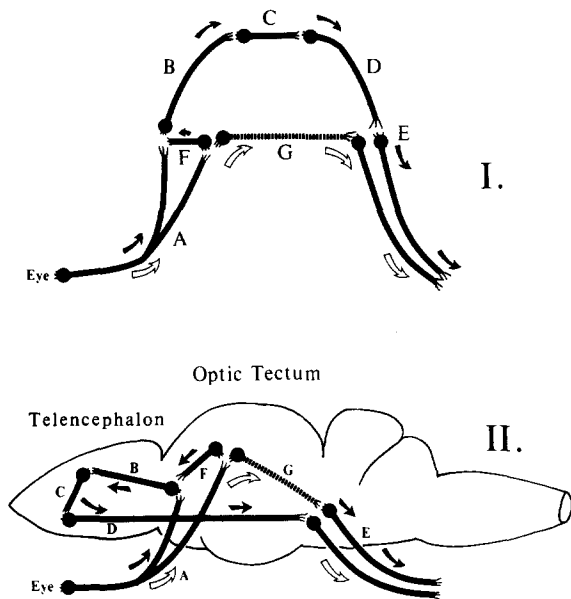


Fig. 5. *I* Schematic representation of hypothetical neuronal network involving sensory input from the eye via (A) to the sensorimotor center of the brain (F), to the center of comprehension (B, C, D), then to the area of neuronal selection (E) – follow solid arrows. A possible short-circuit of this pathway (via G) is represented by the open arrows. *II* Neuronal pathway of *I* superimposed upon schematic representation (lateral view) of a generalized fish brain.

behavioural pathway, may be less plastic: development (e.g. sprouting) and selection of new pathways may be necessary to handle new experiences (a relatively long process). The pace of this development and selection may control the duration of the observed delay in trophic recovery of newly released fish, cited above. Establishing the congruence between the rate of neuronal development (e.g. neuron 'birthdays') and the speed of prey switching behaviour may form a useful test of this hypothesis. Comparing foraging behaviour and brain development in viviparous and oviparous fish may be a useful guide to research of this type.

The brains of fish have specialized areas for long and short-time memory, comprehension and sensory-motor function. It may be possible to study the neuroethological consequences of brain lesions in fish, the results of which may mimic human diseases such as Korsakov's Syndrome and ap-

hasias following stroke. Thus, fish may provide a useful prototype (straight-brain) model for the study of human brain disorders (Campbell & Hodos 1970, Bullock 1983a, 1983b, 1984a, 1984b).

The diurnal rhythms in feeding behaviour presented above imply that subtle aspects of neuronal activity may also affect foraging success and diet choice. Klein & Armitage (1979) have reported 90–100 min oscillations in the abilities of humans to solve verbal and spatial tasks which require mental abilities residing, to some extent, on opposite sides of the brain. These oscillations imply rhythms in brain hemispheric dominance of behaviour. Preliminary studies carried out in our laboratory indicate that handedness (evaluated through asymmetric directions of foraging sorties) occurs in fish, implying hemispheric dominance of behaviour. Diurnal rhythms in feeding error, i.e. error in a behavioural task requiring spatial skill (which may be a unilaterally distributed brain function, as it is in humans), implies that oscillations in hemispheric dominance also occur in fish. These neurological properties may be a source of variance in trophic studies in which timing is uncontrolled.

Diurnal behavioural rhythms may also be manifestations of oscillations in brain function – analogous to those which occur nocturnally during sleep (Kleitman 1963, 1969, Broughton 1975, Klein & Armitage 1979). Wake-sleep rhythms may be an underlying cause of variance in fish behaviour. Sleep in higher vertebrates seems to be associated with the brain's attempt to consolidate memory and eliminate extraneous connections in neuronal circuitry (e.g. Crick & Mitchison 1983). Sleep is of paramount importance in the neuroethology of higher vertebrates and sleep deprivation can have profound consequences. The same may be true of fish; again, fish may present a straight-brain model system for testing hypotheses relating sleep, neuronal structure and ethology. If so, it may be crucial to the proper development of fish that hatchery environments mimic the diel light rhythms of nature. Attempts to enhance growth by keeping fish larvae in perpetual light may frustrate sleep rhythms (but probably not override them entirely) and may promote dysfunctional neuroethological development.

Prolepsis

Fish are not automata, black boxes or stochastic generators of time series data (i.e. behaviours). They, like all animals, are a union of cognitive skills and perceptual ability/limitation (Marcotte 1983). The plasticity of brain development with regard to experience is fundamental to this union as well as establishing an important feedback loop within it.

Three objections are often raised to the inclusion of ideas from the cognitive sciences in ecological theories: (1) it violates simplicity, (2) it violates intuition or (3) it is an anthropocentric imposition. Cognition stands between stimulus and behavioural response. It does not complicate behavioural science; it simplifies it by providing meaning to both the trends and variances (heretofore often considered stochastic, meaningless noise) in behavioural data sets.

Finally, cognition is a plesiomorphic or 'primitive' property of nervous systems – from that of an earthworm, to fish and man (Thorpe 1969). Invocation of cognitive abilities to explain patterns in fish behaviour does not constitute an anthropocentric imposition. It is simply the recognition of the primitive as the primitive: that humans share certain basic processes with other creatures. It is the recognition of the existence of an internal ecology which is responsive to environmental experiences and that these responses alter reactions to future experiences (Hubel & Wiesel 1970, Blakemore 1976, Keating 1976, Blakemore 1977, Cooke & Horder 1977, Keating 1977, Edelman & Finkel 1985). It is the recognition of the reflexive/feed-back relationship between an animal's internal and external ecologies which lies at the heart of adaptive strategies.

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