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Optimizing foraging behaviour through learning

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Manifestation of life-history strategy is through the allocation of resources acquired by foraging. Foraging efficiency can be improved by learning, as fishes adjust their behaviour to changing circumstances. We briefly review the influence of learning on the foraging behaviour of fishes and make recommendations for further research. We stress the importance of quantifying learning and memory in relation to ontogeny and life history.

Key words: Foraging behaviour; learning; memory.

I. INTRODUCTION

Studies of life-history strategy in fishes have largely concerned the allocation of resources to reproduction, growth or some behavioural phenomenon such as migration (for a review see Wootton, 1984). This allocation will be influenced by environmental and biotic factors (Wootton *et al*., 1980). Environmental factors usually concern seasonal variation in temperature, light or salinity, whereas biotic factors involve energy reserves, competition and risk of predation. Before an animal can allocate resources, it must successfully acquire energy, as food.

Foraging behaviour has become a popular subject since economics models were first applied to the problem (Emlen, 1966; MacArthur & Pianka, 1966), leading to the development of Optimal Foraging Theory (OFT) and its various subcategories, including Optimal Diet Theory (ODT) (Charnov, 1976) and the Basic Prey Model (BPM) (Stephens & Krebs, 1986). Like other first-generation OFT models, the BPM is static and makes numerous simplifying assumptions that reduce its applicability to natural situations (Pierce & Ollason, 1987; Hart, 1989). Thus, although in some empirical studies the BPM has successfully predicted observed behaviour (Werner & Hall, 1974; Mittelbach, 1981), in other cases the data did not quite follow predictions and the reasons for this were left to speculation (Kislalioglu & Gibson, 1976*b*; Elner & Hughes, 1978). In yet other studies the model has seriously failed to predict the observed outcome (Hart & Ison, 1991). Static models and associated experiments preclude any temporal effects, such as learning or changes in physiological state, and so can only be considered as momentary representations of an animal's behaviour under prevailing conditions. Werner & Hall (1974) partially avoided this problem by using very short feeding periods. Similarly, Mittelbach (1981) used fish that already had learned the appropriate foraging skills.

More recently, interest has shifted towards the interacting influence of extrinsic and intrinsic factors on foraging decisions (Hughes, 1990). Prey availability

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(Kaiser *et al.*, 1992*a*), predation risk (Milinski, 1979; Magurran, 1986; Godin, 1990), intraspecific competition (Dill, 1983; Hesp, 1990), weather conditions (Burrows & Hughes, 1989, 1990) and changes in internal state (Barnard & Brown, 1981; Lucas, 1990; Croy & Hughes, 1991*a*) are continually changing, as are their consequences for foraging decisions. Realization of this has led to the development of dynamic-programming models, capable of handling the required diversity of variables, including time itself (Houston *et al.*, 1988). For fitness to be maximized against this background of interacting factors, there must exist mechanisms whereby behaviour is continually adjusted. One such mechanism is learning.

II. HOW DO FISH LEARN?

There are three main approaches to studies of learning in fishes. Neurologists have used ablation to locate areas of the brain responsible for learning and memory (Peeke & Gordon, 1981; Ohnishi, 1989). Psychologists have extensively examined conditioned responses using reward (usually food) and punishment (mild electrical shocks) (Breuning *et al.*, 1981; Wright & Eastcott, 1982; Coble *et al.*, 1985; Losey & Sevenster, 1991). Ethologists have measured the effect of experience on the performance of specific tasks (Beukema, 1968; Vinyard, 1982; Dill, 1983; Croy & Hughes, 1991*a*) and this will form the major subject of our thesis (for a review placing different emphasis within this topic, see Kieffer & Colgan, 1992). Most of the neurological and psychological studies are found in journals normally overlooked by fish biologists; hence at this juncture we will examine briefly some of this literature.

NEUROBIOLOGY

Various studies have identified areas of the fish brain responsible for learning (for a review see Martinez & Kesner, 1986). In these areas, the nervous system is modified through experience, leading to the expression of different behaviours. A popular theory is that the modification occurs at synaptic connections between neurons. The specificity of stored information appears to be determined by the location of synaptic change: e.g. all visual information travels first from the eye to a region deep within the brain and from there information referring to pattern and shape passes to the temporal region, whereas spatial information passes to the parietal region (Horn, 1990).

PSYCHOLOGY

Learning behaviour, whether Pavlovian conditioning, instrumental conditioning, imprinting or social learning, often appears to reflect the phylogenetically adapted operation of a basic mechanism, a version of stimulus substitution, whereby inherent behaviour is expressed in response to new stimuli (Suboski, 1988). The shorter the delay between presentation of a new stimulus and access to the reward, the more probable it is that the two will become associated (Olds, 1977). Thus, goldfish, *Carassius auratus* L., learn to recognize new visual cues more efficiently when food is presented simultaneously with, rather than immediately after the cues (Breuning *et al.*, 1981).

Stimulus substitution is susceptible to interference from conflicting information and by stressful conditions. When goldfish have formed a consolidated memory trace of a simple visual pattern, this becomes disturbed if a series of similar patterns is then presented unrewarded, whereas if the confusing patterns are not presented, the fish still respond to the original pattern (Duecker *et al.*, 1980). Stress, in the form of isolation, interferes with memory formation and has possible implications for learning in the presence of predators (Laudien *et al.*, 1986).

Experience gained during ontogeny may influence subsequent learning capabilities. Mecke (1984) found that goldfish raised from eggs in monochromatic light, were unable to discriminate colours in binary choice experiments even after training. Male three-spined sticklebacks, *Gasterosteus aculeatus* L., chase their young to prepare them for encounters with predators and, when compared with orphaned young, showed more effective responses to model predators (Tulley & Huntingford, 1987). Brown (1984) found that naive largemouth bass, *Micropterus salmoides* (Lacépède), fry avoid initially both large and small predators, but after a period of about 6 weeks the fry avoid only the larger predators. These examples indicate the importance of early experience in determining subsequent learning ability.

Learning ability may be related to a fish's size, perhaps through age. Large individuals of the channel catfish, *Ictalurus punctatus* Rafinesque, learned conditioned responses to light and electric shock faster than smaller individuals (Coble *et al.*, 1985). Similar differences are found interspecifically. Carp, *Cyprinus carpio* L., and goldfish learned to reduce the number of mistakes made in simple discrimination tasks based on the colours red and blue, but the larger carp did so more effectively than the goldfish (Henrishfreise & Duecker, 1983). There seems to be no relationship, however, between learning ability and taxonomy. In their study of conditioned responses, Coble *et al.* (1985) found that channel catfish and carp learned more readily than pike, *Esox lucius* L., and bluegill sunfish, *Lepomis macrochirus* Rafinesque. On the other hand, yellow perch, *Perca flavescens* Mitchill, and redbelly tilapia, *Tilapia zilli* Gervais, did not develop conditioned responses.

Despite experimental progress already made, the effects of size, age and phylogeny on learning capability have not been partitioned adequately and the question of why some fish learn better than others remains largely unanswered (Godin & Keenleyside, 1984; Ehlinger, 1989).

III. ETHOLOGY

Fishes clearly are able to use memorized information, revised with experience, as a basis for making behavioural decisions. Here, we consider how this information, acquired through learning, can increase a fish's foraging efficiency.

HABITAT LEARNING

Learning about the habitat is important in terms of homing behaviour (Kennedy, 1981; Helfman & Schultz, 1984), territoriality, refuging and foraging. During ontogeny, habitat requirements may change, with corresponding shifts in responsiveness to categories of habitat. Even when requirements are stable, spatial and temporal changes in habitat are likely to occur, making learning advantageous throughout the life of the fish. This is particularly true with regard to foraging behaviour, since food supplies vary so much in type and productivity. Learning may improve foraging efficiency at two levels, namely the location of food sources and the handling of chosen food types.

Discovery of food sources occurs through sampling and through observation of other foragers (Pitcher & Magurran, 1983; Pitcher & House, 1987). Relocation of profitable sources is made more efficient by learning habitat features that can be used as guides. These may be general features in the surrounding environment that aid geometric position fixing and serve as 'global' cues, or more specific features that may facilitate direct 'beacon homing' and serve as 'local' cues. The distinction between global and local cues, which probably represent the extremes of a continuum in terms of allocation of attention to particular features of the environment, is illustrated by Huntingford & Wright's (1989) account of how three-spined sticklebacks learn to avoid dangerous feeding patches. From a central holding compartment, fish could enter food patches on either side by passing through doors over which were hung distinctive signs. The fish learned to forage in the more profitable patch, but when subsequently threatened in that patch by simulated predatory attack, they learned to favour the less profitable, 'safe' patch. Switching the signs over the doors caused an immediate switch in foraging location by four of the fish. Evidently, these fish had learned to associate local cues, the signs over the doors, with patch quality. The remaining nine fish did not switch, but continued to choose the safe patch. They had not learned to associate the local cues with patch quality, but must instead have used other features, such as lights and pipes on the laboratory ceiling, as global cues. It would be interesting experimentally to examine the basis of such individual variation in use of local and global cues. Is the mechanism analogous to imprinting, whereby a fish continues to use whichever cue first attracts its attention?

The improvement of foraging efficiency through learning is demonstrated by Warburton's (1990) study of the use of local cues by goldfish. In the absence of distinct visual cues, fish visited food sources virtually at random and maintained a high level of exploratory sampling, whereas in the presence of simple, but salient local cues, the fish learned to seek out the productive source accurately and reduced their sampling activity sharply. This concentration on particular cues, however, reduced the fish's ability to adapt to changes in patch profitability.

Habitats differ qualitatively and quantitatively in terms of the visual stimuli they offer as cues. There is ample evidence for well-developed pattern discrimination abilities in fish (Northmore *et al.*, 1978) but little has been done to assess such abilities in terms of how they might facilitate learning and memory in natural situations. It would be instructive to discover to what extent fish inhabiting different environments rely on particular stimuli associated with specific habitats, and whether such preferences are genetically determined. For example, can fish from open, pelagic environments learn to use cues associated with complex, vegetated habitats as competently as fish from complex environments? Such studies could do much to clarify universal features of perception-learning relationships, as well as throwing light on the abilities of fish to generalize important types of habitat stimuli so as to exploit new situations effectively. Can an association with a local feeding cue, for example, be transferred to novel environments?

Inherited differences in habitat-learning ability may be expected at both inter- and intraspecific levels. Interspecific differences in learning ability are discussed above (section II) in relation to phylogeny and body size. Intraspecific variation, presumably genetically based, was reported by Huntingford & Wright (1989), who found that sticklebacks from a pond free of major predators learned to avoid the ‘dangerous’ food source, described above, more slowly than those from a river with abundant predators (see also Huntingford & Coulter, 1989).

In conclusion, there is a need to test and develop foraging models further by examining the role of habitat learning in improving foraging efficiency, especially in relatively complex, multiple-patch environments similar to natural situations. By tending to reduce travel time between patches, effective global and local cues should tend to maximize the average profitability of the environment as a whole and decrease the average time spent in a patch (Cowie, 1977). Alternatively, salient cues may reduce uncertainty and encourage win-stay behaviour (Warburton, 1990). Such work would complement attempts to include learning and memory in models of diet selection and patch persistence (Hughes, 1979; Ollason, 1980; McNair, 1981; Croy & Hughes, 1991*a*). In addition, reports of apparent location learning in fish (Aronson, 1951, 1971; Mariscal, 1972; Warburton, 1990) should be augmented by detailed studies of the factors affecting pattern recognition. There is growing evidence that an ability to orientate using geometric relationships between features in the surrounding environment is the rule rather than the exception (Gallistel, 1989). It is likely, however, that as with other vertebrates (Olton, 1982; Spetch & Edwards, 1988) fish rely on a combination of global and local cues, stereotyped movement patterns (Roitblat *et al.*, 1982) and perhaps route-based navigation using motor cues provided by the animal itself (Kleerekoper *et al.*, 1970; Dodson, 1988).

HANDLING SKILLS

Many studies have addressed the effect of experience on predatory behaviour (Beukema, 1968; Ware, 1971; Thomas, 1977; Hughes, 1979; Croy & Hughes, 1991*a*; Kaiser *et al.*, 1992*a*). In all cases, increasing experience with a particular type of prey increased handling efficiency and hence the net rate of energy intake (Colgan *et al.*, 1986; Ranta & Nuutinen, 1986; Mills *et al.*, 1987; Croy & Hughes, 1991*a*). Handling efficiency can be improved in various ways at different stages in the predatory sequence, from recognition, attack, manipulation to ingestion (Croy & Hughes, 1991*a*).

Foragers may learn to recognize prey types more quickly (Hughes, 1979) by differentiating between certain characteristic features, such as size, colour, shape and presence or absence of appendages (Kislalioglu & Gibson, 1976*a*; Main, 1985; Holmes & Gibson, 1986; Croy & Hughes, 1991*b*; Kaiser *et al.*, 1992*b*). Fast recognition enables fish to be highly selective when foraging among prey that are patchily distributed (Werner, 1974; Kislalioglu & Gibson, 1975). Differences in searching behaviour and capture techniques, reinforced by learning, can lead to individual variations in food specialization (Bryan & Larkin, 1972). However, discrimination may be limited under certain circumstances by sensory constraints. For example, when swarms of prey are encountered, items furthest away from the fish may appear deceptively small. Hence, bluegill sunfish appeared to show only partial preference for the more profitable, larger items when foraging within a swarm of *Daphnia* (Wetterer, 1989).

Capture (attack) efficiency may increase markedly through experience. Ten-spined sticklebacks, *Pungitius pungitius* (L.) presented with a mixture of smaller,

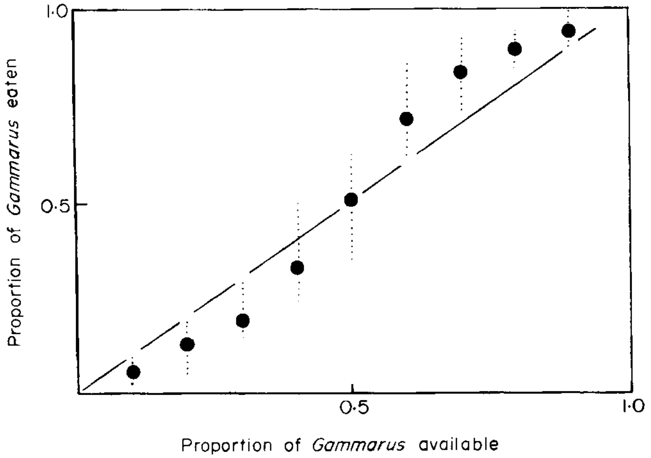

FIG. 1. Frequency-dependent prey selection by fifteen-spined sticklebacks, *Spinachia spinachia*, fed on amphipods, *Gammarus locusta*, and brine shrimp, *Artemia* sp. Data are medians with interquartile ranges.

less profitable, and larger, more profitable *Daphnia*, came to prefer the larger items, with a concomitant increase in the attack–success rate (Ranta & Nuutingen, 1986). Changes in attack mode may be involved, e.g. a switch to burst-speed swimming when attacking fast-moving prey (Nyberg, 1971; Vinyard, 1982; Kaiser *et al.*, 1992*a*).

Manipulation of captured prey is often required prior to ingestion. Generally, this involves reorientation of the prey, removal of appendages or fragmentation of the body to ease swallowing. Skill in performing these acts may improve with experience and although usually highly specific, sometimes they may be transferred within general categories of prey. For example largemouth bass attacked and manipulated live fish more efficiently after having been maintained on a diet of live shrimp than on dead shrimp (Colgan *et al.*, 1986). Prey manipulation may be divided into distinguishable components (Croy & Hughes, 1990), which tend to be reduced in number as experience increases, so reducing the time taken to ingest a prey (Croy & Hughes, 1991*a*). After a period of several weeks feeding on the same prey, the pattern of muscular activity in the jaws may become significantly altered, correlating with increased feeding efficiency (Wainwright, 1986).

As a result of learned predatory skills, the time taken to handle the relevant type of prey decreases, so increasing the yield per unit handling time, or profitability. Learning, therefore, can cause profitabilities of different prey to be transposed in rank (Hughes, 1979) and this could, in principle, cause a frequency-dependent switch in preference (Croy & Hughes, 1990). Frequency-dependent changes in profitability, resulting from learned modification of handling behaviour, have been demonstrated for the fifteen-spined stickleback, *Spinachia spinachia* (L.), feeding on amphipods and brine shrimp (Croy & Hughes, unpubl.). But although the fish switched preference as relative abundances of the two prey changed (Fig. 1), this behaviour did not coincide with the prey frequencies at which profitabilities became transposed (Fig. 2). Further investigation of frequency-dependent learning and associated prey preference, is needed.

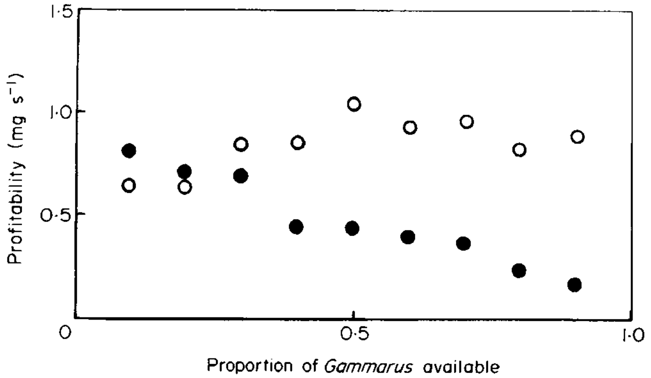

FIG. 2. Frequency-dependent changes in prey profitability (yield/handling time), associated with waxing and waning handling skills as fifteen-spined sticklebacks fed on different mixtures of amphipods and brine shrimp. Data represent yield, predicted from weight-length regressions, per unit handling time, measured in the same trials as in Fig. 1. ○ = *Gammarus*, ● = *Artemia*. (From Croy & Hughes, unpublished.)

PREDATOR AVOIDANCE

When foraging, fish are exposed to mortality risk from predators, altering their behaviour drastically (Milinski & Heller, 1978; Milinski, 1986; Godin, 1986; Magurran, 1986; Godin & Sproul, 1988). Many studies have shown that fish will forage in less rewarding, more complex habitats where risk of predation is lower (Gotceitas & Colgan, 1989, 1990). Mittelbach (1981) found that as the profitability of risky, open-water habitats increased due to a greater abundance of prey, large bluegill sunfish abandoned the sheltered habitat. Smaller fish remained in the weed bed, however, and it may be inferred that potential energetic gains in open water did not outweigh the risk of predation for such small fish. Large sunfish continually sampled both environments, moving into the more risky habitat at a certain threshold prey density. Evidently, even large fish must assess their vulnerability to predation. This learned information may enable fish to optimize their foraging behaviour, not by maximizing the net rate of energy intake, but by maximizing the yield per unit risk of predation (Gilliam & Fraser, 1987; Gilliam, 1990).

SOCIAL LEARNING

Shoaling fish have a unique method of assessing whether a predator is likely to attack (Magurran, 1986, 1990; Milinski, 1990; but see Lazarus & Metcalfe, 1990). This method is inspection behaviour, in which several individuals break away from a shoal to inspect the potential threat (Magurran, 1986). Having assessed the predator's motivation, these ‘ transmitter ’ fish relay the information to the rest of the shoal, the ‘ receivers ’, which thereby learn indirectly about the risk of predation. Inspection behaviour may be controlled genetically, since individual differences in inspection behaviour exist that cannot be explained readily in terms of external morphology, physiological state or sex (Murphy & Pitcher, 1991). Minnows, *Phoxinus phoxinus* (L.), from habitats containing pike, show inspection behaviour towards these predators, whereas those from pike-free waters do not (Magurran, 1990). Csanyi & Gervai (1986) studied passive dark avoidance in response to a predator of four inbred strains of paradise fish, *Macropodus opercularis* L. Differences occurred in the exploratory behaviour during habituation trials, and the impact of the predator varied between strains. Inspection behaviour decays through habituation when the object proves to be non-threatening. Initially, laboratory-reared paradise fish inspected both pike and goldfish, habituating eventually to the goldfish but not to the pike (Csanyi, 1985). Information about food availability also passes from transmitters to receivers in schooling fish and provides the basis of enhanced group-foraging efficiency (Pitcher & Magurran, 1983).

Social fish may require the presence of conspecifics in order to realize their learning potential fully. Thus, fish allowed to group in shoals have been found to learn feeding skills faster than when isolated (Jain & Sahai, 1989). Therefore, in addition to providing the benefits of a transmitter-receiver system, shoaling may reduce the levels of stress detrimental to learning (section II).

SPEED OF LEARNING AND THE MEMORY WINDOW

Speed of learning is more appropriately measured in terms of the number of experiences required, rather than the time it takes to complete the learning process. This allows species with different physiological time scales to be compared directly. Thus we find, for example, that paradise fish learned to avoid completely a location associated with electric shock after a mean of eight trials (Csanyi & Gervai, 1986). Huntingford & Wright's (1989) sticklebacks learned their aversive response to perceived predation risk completely, after eight trials. Fifteen-spined sticklebacks learned fully developed handling skills for new prey after five to eight trials (Croy & Hughes, 1991*a*). The fact that learning is completed within about five to ten trials in animals as different as fishes (above), crabs (Cunningham & Hughes, 1984) and snails (Hughes & Dunkin, 1984), suggests that a fundamental neurological process is involved (section II). On the other hand, the completion of learning in psychological experiments sometimes requires hundreds of trials. For example, visual and spatial probability learning in goldfish took over 200 trials to reach an asymptote (Mackintosh *et al.*, 1971). This discrepancy perhaps derives from the highly artificial tasks often presented in psychological experiments.

The relative change in performance on completion of learning, i.e. learning efficiency, is proportional to the salience and number of available cues associated with the learned response and the relevance of such information to the needs of the animal. The accuracy, as a proportion of correct visits achieved by goldfish learning to discriminate between productive and unproductive patches, decreased from 1·0 with simple, 'direct' cues adjacent to the food source, 0·9 with simple 'indirect' cues marking the empty patch, to 0·7 with a structurally complex cue next to the food source (Warburton, 1990). Fifteen-spined sticklebacks reduced the handling time for amphipods by 68% when these were presented in mono-specific runs, but only by 59% when presented alternately with brine shrimp (Croy & Hughes, 1991*a*).

Learning efficiency is also likely to depend on the extent to which other imperatives, such as predator avoidance and competitive interactions, vie for the fish's attention. In gregarious foragers, the risk-balancing trade-off between foraging and vigilance varies with shoal size (Pitcher & Magurran, 1983), suggesting that in larger groups the fish are able to attend to relevant stimuli better (Smith & Warburton, 1992). In competitive situations, subdominants may be denied choice, despite any learned information about the environment. Smaller, subdominant fifteen-spined sticklebacks, for example, gave up sampling between food sources when in the presence of larger, dominant fish, and took whatever prey the dominants missed (Croy & Hughes, 1991*b*).

Memory in fishes has received far less experimental attention than learning and there is little information on its duration in relation to the nature or complexity of learned information [an exception is the work of Miklosi *et al.* (1992), discussed below]. Moreover, reported differences are too inconsistent for a pattern to emerge. For example, learned prey-handling skills were retained only for 3 weeks by fifteen-spined sticklebacks, but for as much as 2–6 months by salmonids (Bryan & Larkin, 1972). Length of the memory window is a most important variable that presumably is at least partly under genetic control and therefore susceptible to natural selection. It should be proportional to the relevance, generality and consistency of the learned information. The features of a predator, noticed during an attack, perhaps may be remembered for life, whereas the location of a transitory food source may be remembered only for the duration of the foraging bout. Decremental importance placed on past experience is an important theoretical concept in certain models of foraging behaviour (Lester, 1984) and is adaptive where changing circumstances require information to be updated continually. In agreement with these predictions, Miklosi *et al.* (1992) found that male paradise fish remembered the individual identity of sexual competitors only for about a week, but remembered the general identity of goldfish for at least 3 months. Paradise fish breeding territories are reorganized approximately once a week, so that memorized identity of neighbouring males if relevant only within this time span. Heterospecific fish, on the other hand, represent potential predators and so information about them remains relevant for life.

IV. CONCLUSIONS

At the beginning of this paper we said that the status of energy reserves would be important in the manifestation of life-history strategy, which therefore is dependent on foraging efficiency. Fish live in heterogeneous environments; on a small scale they encounter variation in food distribution, whereas on a larger scale, habitat is continually changing for migratory and intertidal species. We have shown that under a wide variety of circumstances, fish can improve their foraging efficiency with experience. Learning therefore permits adaptive behavioural flexibility (Dill, 1983; Hart, 1989).

Fish must evaluate new prey, food-patch quality, predation risk and competitive situations continually. Accordingly, they improve handling techniques rapidly when encountering new prey, learning to choose appropriate attack modes (Nyberg, 1971; Helfman & Winkelman, 1991; Kaiser *et al.*, 1992*a*), and to eliminate unnecessary handling procedures (Croy & Hughes, 1991*a*). Fish tend to examine novel objects in order to evaluate their food or threat potential (Magurran, 1986, Csanyi *et al.*, 1989). Moreover, fish have been shown to avoid richer food patches associated with higher predation risk, (Mittelbach, 1981; Ehlinger, 1989; Croy & Highes, 1991*c*). In so doing, they incur the cost of a lower rate of food intake in safer, less productive or more complex habitats, but this is traded off against the lower probability of being attacked by predators (Ehlinger, 1989; Gotceitas, 1990; Gotceitas & Colgan, 1990). Correlations between environmental heterogeneity, diet breadth, learning ability, memory, inter- and intra-

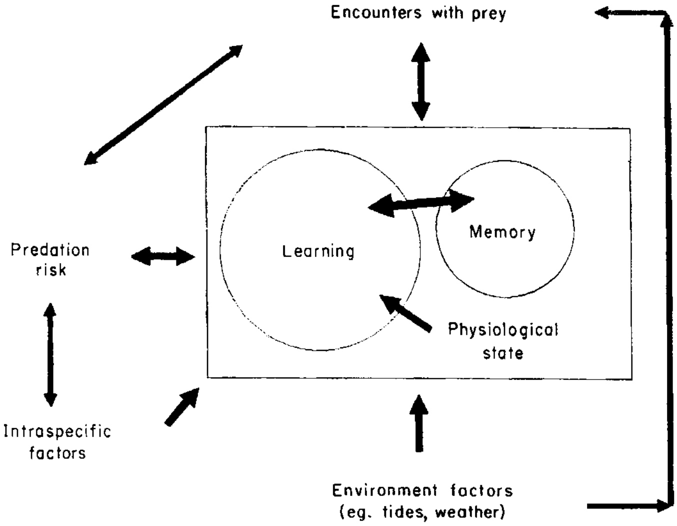

FIG 3. Relationships between some of the factors that affect learning in fishes.

specific interactions and physiological state may help to elucidate these complex interactions (Fig. 3).

Foraging skills are retained for up to 3 weeks, a much longer time than it takes to acquire them (Croy & Hughes, 1991*a*,*b*). The fact that fish learn so quickly, but only retain certain learnt skills for a relatively short period of time, indicates how rapidly their environment changes. Fish seem to remember experiences with predators for much longer periods than encounters with prey items. Perhaps because the type and size range of availability prey alter continually during fish growth, short-term memory is sufficient. This short-term memory depends on the number of subsequent encounters with the same prey (Croy & Hughes, 1991*a*). In the particular case of the fifteen-spined stickleback, new prey may be encountered on consecutive tides (Kaiser & Hughes, 1992). Some prey, such as amphipods, are resident and regularly encountered, so associated handling skills will be remembered for relatively long periods. Others, e.g. swarms of mysids, are encountered infrequently but in large numbers at a time. Therefore, handling skills for these prey are likely to oscillate through learning and forgetting. Thus memory may be expected to have variable duration, determined by the relevance of the information as a function of time. This function will depend not only on the nature of the information itself (e.g. habitat features, characteristics of prey type and distribution, identity of predators), but also on changing size and morphology of the forager during growth and, perhaps, on life span. Hence, ontogeny and life history might be related to learning ability and the length of memory windows. How do these properties in small, short-lived fished compare, for example, with those in larger, longer-lived species? There is scope here for much productive research.

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