THE PREDATORY BEHAVIOUR OF RAINBOW TROUT
(SALMO GAIRDNERI)

by

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B.Sc., University of British Columbia, 1966

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in the Department

of

ZOOLOGY

We accept this thesis as conforming to the

required standard

THE UNIVERSITY OF BRITISH COLUMBIA
JANUARY, 1971

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ABSTRACT

The predatory behaviour of rainbow trout was studied to identify some of the major factors that influence their response to prey. Two benthic-living amphipods _Crangonyx_ sp. and _Hyalella_ sp. were selected as representative prey. In some experiments, artificial food was utilized.

Rainbow trout adopt a searching position some 10 to 15 cm from a substrate and locate food visually. As a result, they can detect only organisms that are exposed. In the presence of a complex substrate, trout were able to recognize moving prey with greater success (74%) than stationary targets (39%) with the same visual characteristics. The distance from which trout will react to food was shown to be dependent upon the size, inherent contrast and activity of the object as well as the ambient illumination, turbidity of the water and complexity of the substrate. After 6 to 7 days of experience with a new but palatable food, trout can increase their reactive distance through learning. A general system of equations was developed to describe the effect of each of these parameters on reactive distance.

On the average, trout successfully capture 82% of the prey they attack. In the laboratory, the rate of capture reached a maximum level when the density of prey was increased to 240 animals per sq. m. Irrespective of the abundance of food, however, decreasing hunger motivation was found to depress the predator's rate of capture as was the presence of a substrate in which the

prey could conceal themselves.

The effect of water temperature on the vertical and horizontal movements of _Crangonyx_ and _Hyalella_ was also examined. The vertical activity of both prey increased exponentially with a rise in temperature. In contrast, 10° C. was suggested to be the optimum temperature for the movement of exposed animals.

A general simulation model was developed to test the hypothesis that the selective exploitation of 4 major invertebrate groups in Marion Lake, by trout, occurs at the perceptual level. The model considered the predatory behaviour of the fish as well as the density and physical characteristics of their prey, and was able to predict with some accuracy the occurrence of different foods in trout stomachs.

The model was also able to account for the size - selective exploitation of _Crangonyx_ and _Hyalella_, the seasonal changes in the vulnerability of these species, and the fact that the less numerous _Crangonyx_ was captured just as frequently as _Hyalella_.

Trout require a threshold rate of capture (about 2 captures / min.) to maintain a specific pattern of search. If they do not attain this threshold they will switch their attention to other hunting patterns. As a result, the population should converge, temporarily, into areas in which food is relatively more abundant. Since trout can also learn to increase their responsiveness to prey, both of these characteristics would

improve their hunting efficiency.

The results of this study indicate that visual predators will discover and, subsequently may exploit, large prey that tend to be exposed and active, with greater success than smaller, less active or less conspicuous species. Moreover, if a visual predator maintains a searching position, it may not detect benthic-living food organisms less than a critical size. The significance of these conclusions is discussed.

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GENERAL INTRODUCTION

Many laboratory studies have been conducted to describe
the feeding behaviour of animals (De Ruiter, 1966); very few
of these,however, have attempted to predict how natural populations
of predators will exploit different species of prey.

Until very recently, the method of how to systematically
relate laboratory studies to the field was rather elusive. In
1966 however, Holling described what he called the "experimental
components analysis". This approach is based upon the premise
that a biological process, such as predation, can be broken down
into fragments. These components can then be studied under
controlled conditions to elucidate their importance and relationship
with other parts of the process. The structure of the resulting
system is not assumed to be a complete explanation or description
but rather is designed to be continually modified in the face
of new observations and experimental results. In essence then,
the system becomes a working hypothesis that can be tested either
in the laboratory or on natural populations.

In this study I have attempted, through laboratory experiments,
to analyse the feeding behaviour of rainbow trout. The first
section of the study is devoted to a general description of their
behaviour and some of the major components which affect it. This
analysis is continued in the second section and takes the form
of a single question: can trout learn to alter their response
to prey? In the third section, I will describe the effect of
water temperature on the activity patterns of two species of
amphipods (Crangonyx richmondensis and Hyalella azteca) that are

natural prey of rainbow trout, and develop a vulnerability

submodel.

The final section will examine the relationship between the

visual characteristics of prey in general and the process of prey

detection. Various aspects from the manuscript will then be

coupled into a simulation model to attempt to account for the

selective exploitation of several major invertebrates, but

especially the amphipods, by the trout population in Marion Lake.

SECTION I

THE EFFECT OF PREY DENSITY, PREY SIZE AND THE PRESENCE OF
A SUBSTRATE ON THE FEEDING BEHAVIOUR OF TROUT

INTRODUCTION

In most aquatic systems it appears as a generalization that
fish tend to exploit exposed prey to a greater extent than less
conspicuous species (Grimas, 1963; Allen, 1941). There are
other factors, however, besides the degree of exposure which
will determine the rate predators exploit prey. These factors
can be divided into 3 specific categories:

1) the characteristics of the prey (i.e. size, density
   and behaviour),

2) the feeding behaviour of the predator (i.e. searching
   behaviour, and the mechanisms it utilizes to locate
   and capture food),

3) the characteristics of the environment (i.e. the
   ambient illumination, temperature and physical
   structure).

Allen (1941) stressed the importance of the characteristics
of prey. He suggested that since different species have different
dispersal and behavioural patterns, are different sizes and exist
at different densities, they are not likely to have the same
probability of being detected and captured by predators.

The tactics that predators employ to locate and handle food
also contribute to determining predation rates (Ivlev, 1961;
Holling, 1966). These tactics, however, may be modified through
hunger motivation and in some cases through learning (Holling,
1965; Holling, 1966; Beukema, 1968).

There is also considerable evidence to indicate that predation is affected by environmental factors such as the ambient illumination (Ali, 1959; Hunter, 1968; Blaxter, 1968a) and the physical complexity of the environment (Ivlev, 1961; Macan, 1966; Johannes and Larkin, 1961).

The purpose of this study was to examine the effect of 4 factors: 1) prey density, 2) prey size, 3) hunger motivation and 4) the presence of a substrate on the feeding behaviour of rainbow trout (Salmo gairdneri). Feeding experiments were replicated with 2 different species of amphipods as prey (Crangonyx richmondensis and Hyalella azteca).

The study was divided into 4 parts to systematically construct a descriptive equation of the effect of each of these components on the behaviour of trout. The first 3 sections will consider the influence of the aspects mentioned above on the rate of prey capture, while the final section will examine the relationship between the trout's rate of capture and searching behaviour.

METHODS AND MATERIALS

Four rainbow trout, obtained from Marion Lake, British Columbia, were used in this study. They ranged in length from 13.4 to 17.0 cm. Each fish was held in isolation between experiments in a 227 litre (50 gallon) glass aquarium. Two other identical tanks were utilized for predation experiments.

In both the holding and experimental tanks, the water temperature was maintained at 10 C ($\overset{+}{-}$ 2 C). Although the background illumination was natural, it was 'controlled' by avoiding direct light and conducting experiments at the same time of day (1200 to 1400 hrs P.S.T.).

Four different substrates were employed to test the effect of physical complexity on predation. The characteristics of each of these treatments are described in Table 1. The control substrate was simply a bare, grey colored surface. The litter I and II treatments, on the other hand, were composed of large pieces of stick litter and covered, respectively, 6% and 15% of the tank bottom. The fine litter treatment was the most complex utilized as it covered the entire floor of the tank. This material was obtained by screening sediment from Marion Lake to remove both the very fine and the very coarse particulate matter. This was necessary to facilitate the recovery of prey and to insure that the substrate would settle rapidly if it was disturbed by the feeding activity of the predator.

The behaviour of trout was examined at a minimum of 3

different densities of prey in each of the 4 substrate treatments.
Predation experiments were replicated independently for both
species of amphipods (Table 2). The response of trout to
juvenile Crangonyx was also investigated but only in the litter
II treatment. As a result, the effect of prey size on predation
could be assessed by comparing the results of these experiments
with those obtained when adult Crangonyx were in the same
situation.

To observe the feeding behaviour of trout, in different
states of hunger motivation, and yet insure that they would not
capture enough prey to reach satiation, different densities of
Crangonyx and Hyalella were utilized. Preliminary results
indicated that the trout would become satiated after consuming
about 90 standard sized adult Crangonyx (Table 3). To reach
the same state, they would have to capture over 200 smaller,
Hyalella. Therefore, the density of each prey was regulated
so the number captured during an experiment did not exceed
these respective limits. The range in density of juvenile
Crangonyx was identical to that choosen for Hyalella, as they
are both of similar size and to some extent weight (Table 3).

The hunger level of the trout was standardized by depriving
them of food for 48 hours before an experiment (in a few instances
this period lasted as long as 96 hours). Some preliminary results
indicated that the fish required 50 to 60 hours at 10 C. to
completely digest a satiation ration. Since the amount of food
they were able to ingest in virtually every experiment was well
below their satiation level, 48 hours of deprivation should have

been adequate to clear the digestive tract of all food material between succesive feedings.

The experimental procedure consisted of gathering the required number of prey from Marion Lake and holding them, without food, in plastic containers for up to 24 hours. The feeding tank was prepared by adding a standard sample of substrate material and spreading it uniformly over the bottom. The prey were then introduced and allowed 60 minutes to disperse before a predator was released. Specific aspects of the trout's feeding behaviour were recorded chronologically on a Rustrack, 4 channel recorder (Model 921).

The experiments were terminated after 50 minutes at which time any prey remaining in the tank were recovered and counted. This residual density was subtracted from the initial density to determine the number of amphipods captured. The recovery technique was tested and was found to be 97% to 100% efficient in recovering prey, therefore, no correction was made for any loss of animals during this operation.

TABLE 1.   Characteristics of the experimental substrates

Treatment	No. objects or depth *	Average object size	Surface area (cm^2)	Area of tank bottom covered (cm^2)
Control	0	0	4180	0
Litter I	34	(6x1x1) cm.	4700	253
Litter II	47	(9x2x1) cm.	5487	640
Fine Litter	4mm.	(0.4-0.7) mm.	4180+	4180

*see text

TABLE   2. A representation of the experiments conducted to determine the effect of a substrate and prey density on the feeding behaviour of trout. The column figures indicate the number of replicate experiments conducted with different fish.

| | Prey Density | | | | | | | | | | | | |
| | Adult Crangonyx | | | | | Adult Hyalella | | | | | Juvenile Crangonyx | | |
Substrate	20	40	70	100	200	20	40	70	100	200	40	100	200
Control	-	2	2	-	-	2	2	1	2	2	-	-	-
Litter I	1	2	2	1	-	-	2	-	2	2	-	-	-
Litter II	-	2	2	2	-	-	2	-	2	2	2	2	2
Fine Litter	-	2	-	2	2	-	2	-	2	2	-	-	-
No. exp.			22					27				6	

TABLE 3.   Average lengths and dry weights of individual prey used in the predation experiments.

Prey	$\overline{X}$ Length (mm) *	$\overline{X}$ Dry weight (mg)
Adult _Crangonyx_	8.1 ± 1	2.6
Juvenile _Crangonyx_	4.6 ± 1	0.5
Adult _Hyalella_	5.7 ± 1	1.0

* the range in length is indicated

RESULTS

GENERAL FEEDING BEHAVIOUR

Rainbow trout appear to locate food visually. This was
verified by observing the behaviour of both wild and experimental
fish. In either case, their attack response comprised three
distinct steps; orientation, visual fixation, and a rapid,
direct attack. This is a common pattern and has been observed
for other visual predators (Messenger, 1968; Holling, 1966).

When trout hunt for benthic prey, either in the laboratory
or in the field, they search from a position some 10 to 15 cm
above the substrate but orient downward to face it. This
characteristic incline (about 10 to 20 degrees) might be to
direct their visual axis onto the sediment, since it is slightly
oblique to the longitudinal body axis (Polyak, 1957).

A fish will search from this characteristic position with
monocular vision. As a result, it will detect most targets at
an angle (lateral) to its path of search. Once a target has
been detected the trout will orient to face the object and then
pause momentarily to fixate it with binocular vision before
attacking. When the attack occurs, it is rapid and is followed
immediately by a strike and engulfment of the prey. The predator
will then return to its searching position before it resumes
hunting. A complete attack sequence may require only 2 seconds.

Rainbow trout are not always successful in discriminating
between prey and 'similar' objects, they will strike at pieces
of stick litter. When they react to an inanimate object they
will strike at and reject it several times before their attack

response is terminated. This indicates that trout probably rely upon either tactile or chemical discrimination to distinguish between food and inedible objects.

Even this very cursory description of their feeding behaviour implies that as long as trout hunt from a position some distance from the sediment and rely upon vision to locate food they will detect only exposed animals. This supposition will be examined in more detail below.

The Effect of Hunger and Prey Density on the Rate of Attack
(Control Experiments)

It is well documented that the feeding motivation of many animals is affected by food deprivation. Ishiwata (1968b) found that the amount of food rainbow trout would consume, feeding _ad libitum_ after various periods of food deprivation, was inversely related to the amount which remained in the stomach from the previous meal. If hunger is defined as an animal's motivation to feed, it may be expressed as:

$$(1) \quad H_t = 1 - (Vt / V_{max})$$

where (H_t) is the level of hunger at time (t), (V_{max}) is the stomach capacity and (Vt) is the amount of food in the stomach at time (t). Hunger will, therefore, be greatest (numerically, 1) when the stomach is empty, and minimal (numerically, 0) when it is full.

This expression of hunger is convenient in that it allows one to quantify an animals feeding motivation at any time if the amount of food in its gut is known. It is also, however, extremely simplistic with respect to the complex mechanisms which are known to affect feeding motivation (Ruch and Patten, 1965). For example, it does not account for time lags in physiological feedbacks such as blood sugar levels but implicitly assumes that the state of hunger will change immediately after any food is ingested or alternately, cleared from the stomach. With these restrictions in mind, equation (1) can be used to investigate the relationship between hunger and the feeding behaviour of rainbow trout.

The satiation ration, or the maximum stomach capacity of the fish was determined by holding them in isolation until all the food consumed during their previous meal had been passed from the digestive tract. They were then allowed to feed ad libitum until they reached satiation (stopped attacking prey). Since the number of amphipods captured during this period

and the average weight of a single animal were known, the amount
of food each fish consumed could be estimated. The results of
these experiments indicated that the trout became satiated
after consuming 230 mg. dry weight, (1 S.E. $\pm$ 12 mg.),
regardless of whether they were fed adult Crangonyx or
Hyalella.

In the predation experiments, captured prey were not
replaced. Therefore, both the density of prey as well as
the predator's level of hunger declined as the experiment
progressed. Either of these aspects could affect the rate
at which trout attack, therefore, the control experiments
were pooled according to the type of prey and were analysed
by multiple linear regression. For this analysis, an experiment
was divided into 30 second intervals so the density of prey and the
state of hunger of the trout at one interval (t) could be
correlated with the rate of attack in the succeeding interval
(t + 1). The level of hunger at the beginning of each time
period could be estimated (equation 1) as both the number of
prey that had been captured up to that point and the average
weight of each of the test prey were known (Table 3).

A regression analysis indicated that prey density and hunger were positively correlated with the attack rate (Table 4). In other words, as the density of prey decreased the rate of attack diminished but at a rate that was dependent upon the trout's level of hunger. An example of the progressive decline in the attack rate from one series of experiments is illustrated in Figure 1.

Observation suggested that the negative feedback between hunger and the rate of attack might have been due to an increase in the amount of time trout use to handle food as their hunger diminishes. Hunger has a similar effect on handling time in mantids (Holling, 1966).

On the basis of the control experiments, the relationship between prey density (PD), hunger (H_t) and the rate of attack (RA) was found to be adequately described by the regression equation:

$$(2) \quad RA = b_1 \ (PD) \ + \ b_2 \ (H_t) \ + \ K$$

The effects of prey density and hunger are indicated, respectively, by the constants (b_1) and (b_2) ; (K) is the Y-intercept of the regression.

In the control experiments the value of (b_1) was significantly larger when Crangonyx were prey (Table 4). This means that when both species were at comparable densities, trout attacked Crangonyx more rapidly than Hyalella. One possible explanation for this result is explored below.

Figure 1. The progressive decline in the rate of attack

(30 second intervals). The results presented are from

2 control experiments in which the initial density of

prey was 200 _Hyalella._ The closed circles indicate

the rate of attack of one fish; the open circles, the

attack rate of another fish.

Hyalella (control)

Rate of attack (no./sec.)

Time (min.)
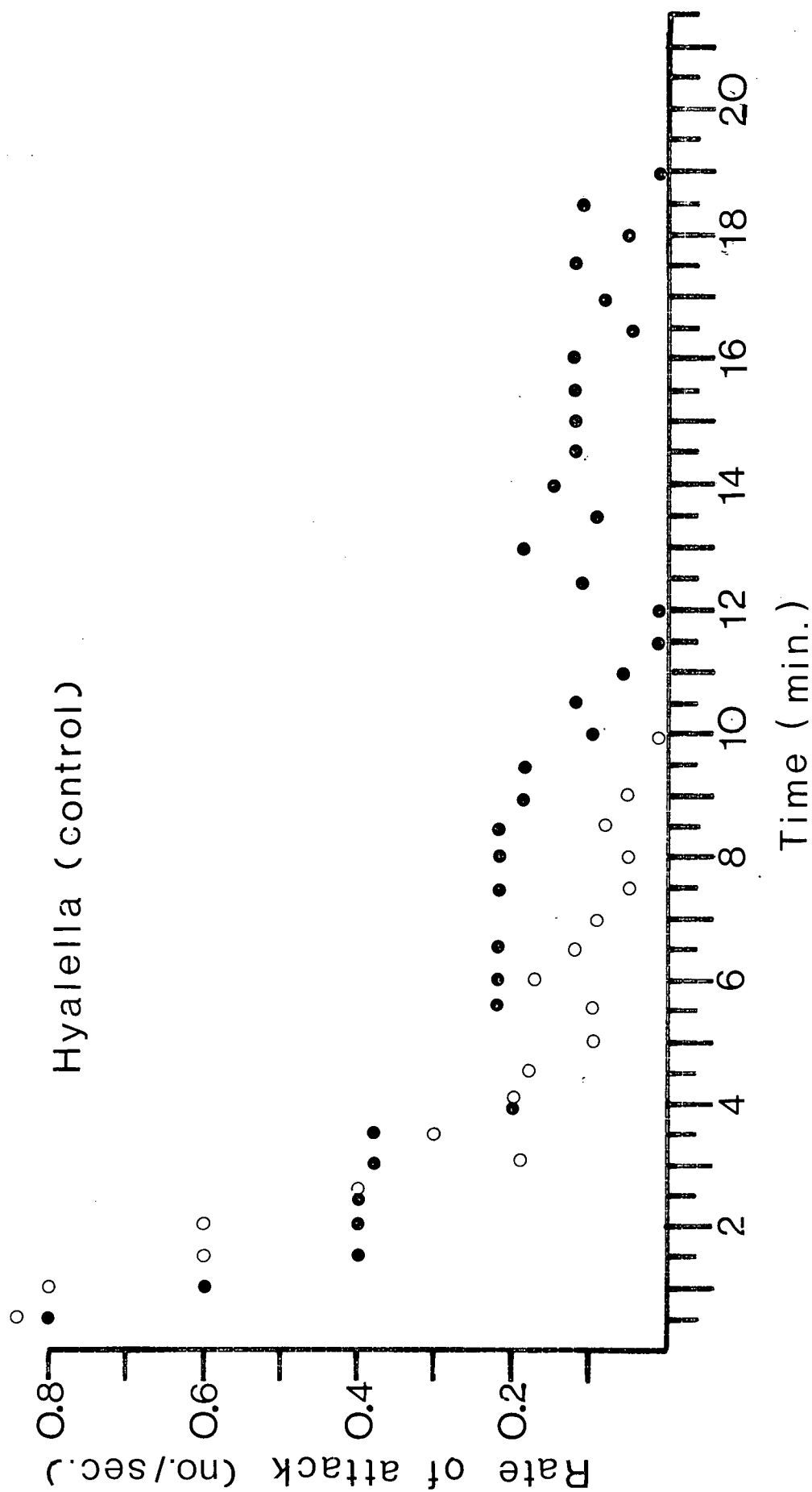
TABLE 4. Regression constants for the rate of attack at time (t) with respect to the hunger level of the trout and the density of prey 30 seconds earlier. The constant (b_1) indicates the effect of prey density on the rate of attack; (b_2) the effect of hunger and (K) the y-intercept. The standard deviation of each of the constants and the partial correlation coefficients (r) are indicated. R^2 is the total amount of variability accounted for by each regression. (n) indicates the number of time intervals obtained by pooling all the experiments (Exp.) from each treatment.

TABLE 4

Prey	Exp	n	Density (b_1)	Hunger (b_2)	K	R^2
			Control			
Hyalella	9	93	0.0024 ± 0.0002	0.474 ± 0.064	-0.207	0.66
r			0.71	0.62		
Crangonyx	4	50	0.0045 ± 0.0005	0.360 ± 0.044	-0.13	0.83
r			0.78	0.77		
			Litter I			
Hyalella	6	78	0.0023 ± 0.0003	0.345 ± 0.072	-0.178	0.57
r			0.62	0.49		
Crangonyx	6	52	0.0075 ± 0.0005	0.145 ± 0.035	-0.05	0.88
r			0.89	0.51		
			Litter II			
Hyalella	6	65	0.0028 ± 0.0002	0.241 ± 0.067	-0.19	0.62
r			0.81	0.42		
Juv. Crangonyx	6	66	0.0026 ± 0.0003	0.326 ± 0.162	-0.13	0.50
r			0.68	0.65		
Crangonyx	6	51	0.0053 ± 0.0009	0.223 ± 0.061	-0.13	0.62
r			0.65	0.46		

The Relationship Between the Rate of Attack and Prey Size

The rate a predator will encounter food is determined largely by: 1) the distance from which it will react, 2) the density of prey, and 3) the relative velocity between the predator and prey (Holling, 1966). The fact that Crangonyx was attacked at a faster rate than Hyalella, could be accounted for if either the searching velocity of the fish, or the distance from which they attacked was dependent upon the type of prey to which they were exposed.

Both species of amphipods move relatively slowly with respect to trout; therefore, in this case, the velocity of the predator will contribute most to determining the rate of encounter. The range in velocity at which trout searched for Crangonyx, was determined in each of the control experiments (fig. 2). This component was expressed simply as the amount of time the predator took to cover a known distance when it was in its characteristic searching position. Although the average velocity at which the fish searched for Hyalella was not measured, there was no apparent indication that it changed.

The distance from which a predator will react to prey will also determine the rate of attack. Brawn (1969) found that cod can detect large prey from a considerably greater distance than smaller prey. An independent set of experiments was conducted to investigate the possibility that the reactive distance of trout was related to prey size. In order to measure this distance, I introduced a single prey of known size into one of the experimental

tanks before releasing a fish. The reactive distance was defined as the distance between the predator and prey when the trout initiated an attack. The results of these experiments (Table 5) clearly indicate that the distance of reaction is dependent upon prey size. This relationship might be sufficient to explain why adult Crangonyx, the larger of the two species, was attacked at almost twice the rate as Hyalella. In all other respects, except their size and activity, these animals are very similar.

In the control experiments every amphipod was exposed and captured before an experiment was terminated. Under these conditions, the density of prey, their size, as well as the state of hunger of the trout affected the rate of attack. In the presence of a litter substrate, however, the feeding behaviour of the predator, the dispersal behaviour of the prey, or both might be somewhat altered. These possibilities are considered in the next section.

Figure 2. The searching velocity of rainbow trout in
    several control experiments. See text for further
    explanation.

FREQUENCY

SEARCHING VELOCITY
(cm/sec)
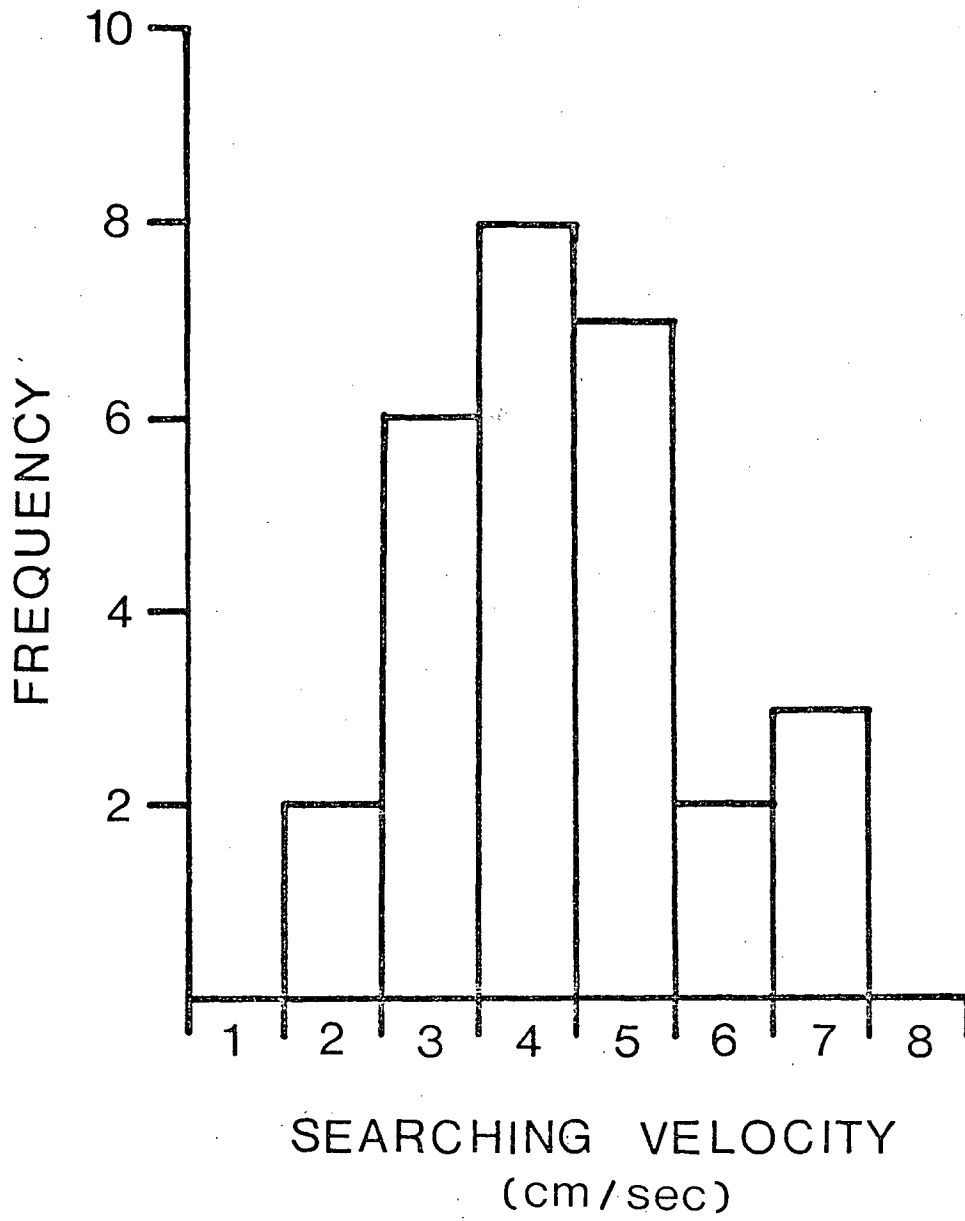
TABLE 5. The relationship between reactive distance and prey size. The prey were live Crangonyx. (n) indicates the number of observations obtained from 2 fish. The average reactive distance is expressed to the nearest significant figure. The 95% confidence intervals are presented.

Prey Length (mm)	n	Mean reactive distance (cm)
4	9	18 ± 3
5	17	22 ± 2
6	9	28 ± 5
7	21	28 ± 3
9	28	35 ± 3

THE EFFECT OF A SUBSTRATE ON THE ATTACK RATE
(LITTER EXPERIMENTS)

Before a fish was released the prey were introduced into the experimental tank and were allowed one hour in which to disperse. When litter was present some amphipods would conceal themselves immediately by moving under any object they encountered. Other animals would move about for some time before they took cover or else failed to move under cover at all. The result of this behaviour is that at any instant in time the number of prey that were exposed was determined by the rate at which animals were both leaving and entering concealment.

An experiment was conducted with adult <u>Crangonyx</u> to determine if they would establish an equilibrium level of exposure, and if so, how long it would take. Four populations of amphipods were introduced into separate containers of water (25 cm in diameter). Each vessel had 18% of the bottom area covered with stick litter identical to that composing the litter I and II substrates. The populations were then observed for over an hour. Without exception, the proportion of animals that were exposed declined rapidly in the first 45 minutes after they were introduced until an apparent equilibrium was reached (fig. 3). Although the length of time concealed animals remained under cover proved to be relatively long, some did re-expose themselves. The same animals were not continually exposed or concealed. On the basis of these observations, it was concluded that the hour in which the prey were allowed to disperse before an experiment was likely sufficient for the test population to reach an equilibrium level of exposure before the

Figure 3. The average time required for four experimental
populations of <u>Crangonyx</u> to reach an 'equilibrium' level
of exposure. The data points are means of 4 replicates.
The curve was fitted by inspection.
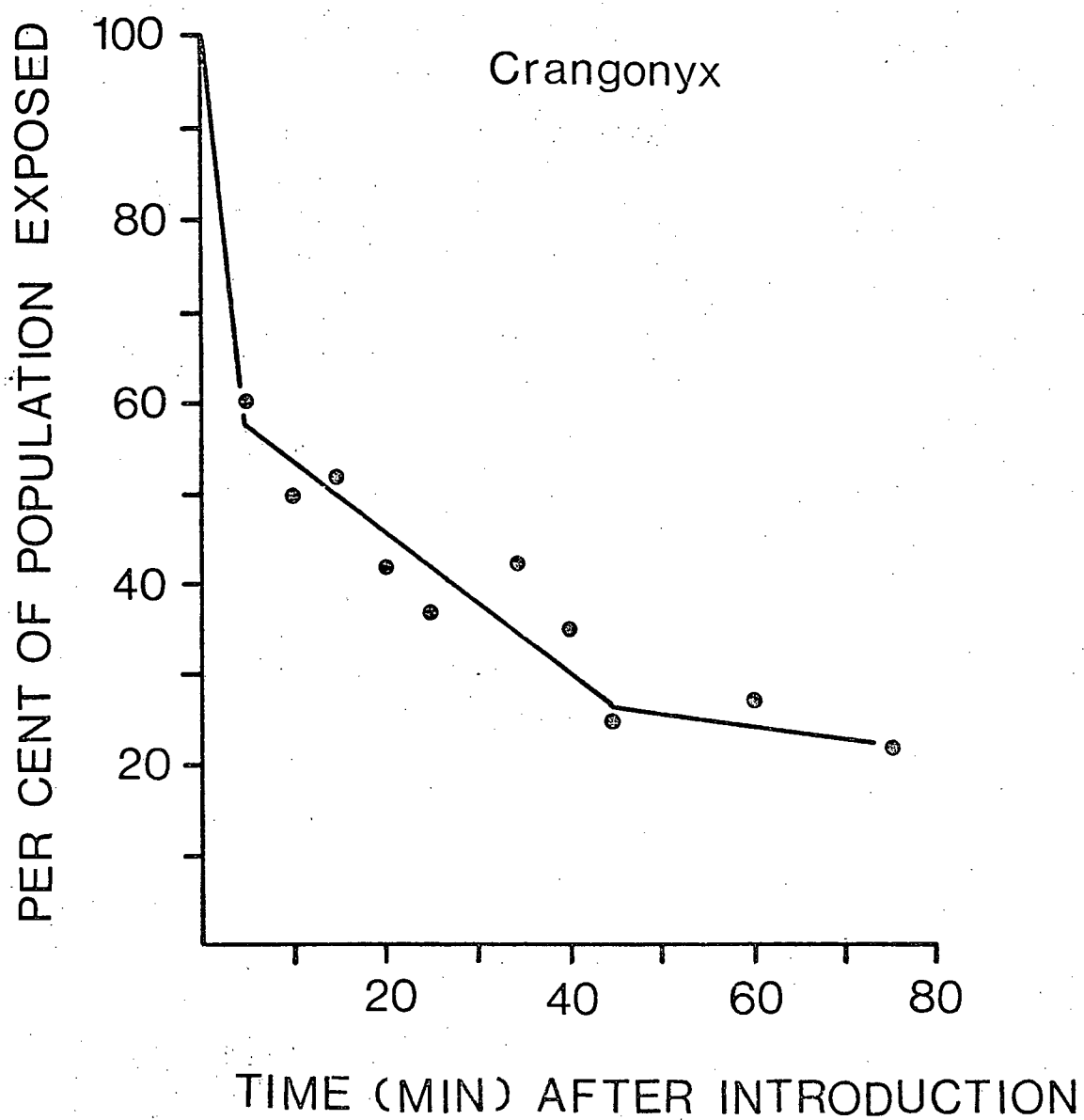
predator was introduced.

The feeding behaviour of trout was essentially the same when a substrate was present as it was in the control situation. In both cases, the fish maintained a searching position and responded visually to prey. During the 50 minute duration of the litter experiments the trout did not disturb the sediment or move pieces of litter to find food, they only captured animals that were exposed. Figures 4 and 5 illustrate the relationship between the number of prey that were captured and the type of substrate. It is evident that at each of the experimental densities a greater number of Crangonyx and Hyalella were concealed and therefore were invulnerable to predation when more cover area was available.

These results (figs. 4 and 5) were fitted by linear regression and without exception, were described adequately by a straight line which passed through the origin (Table 6A). This indicates that the proportion of animals that were exposed in each treatment (PE), which is given by the slope of the line, was constant over the range of densities used. In the litter II series the number of adult and juvenile Crangonyx that were captured when both populations were of comparable size was not different so these two sets of data were pooled.

The length of time an amphipod requires to locate cover should be directly proportional to the amount of stick litter. If the amount of cover area is increased but the average length of time an animal remains concealed or exposed does not change, then the proportion of prey in the population that are exposed

should diminish accordingly. This might explain the inverse
relationship between the amount of cover area and the proportion
of prey that were captured when a substrate was present.

This may not be a complete explanation, however, as there
was a substrate-species interaction (Table 6 B). Fewer Crangonyx
were captured in the litter II treatment, while Hyalella was
less vulnerable in the fine litter experiments. Nevertheless,
the number of prey that were vulnerable to attack and therefore
the attack rate were related to the type of substrate.

If the rate of attack during the litter experiments is
analysed in the same fashion as the control results, only in
this case, the population density is expressed in terms of the
density of vulnerable prey at time (t), it is possible to
determine if the presence of a substrate directly affected the
feeding behaviour of the fish other than indirectly through
prey density. If it did not, then the values of b_1, b_2, and K
that are obtained by a multiple regression analysis of the litter
experiments should be similar to the values obtained in the
control situation. The fine litter treatment was not analysed
because it was difficult to accurately discriminate between
attacks trout directed at prey and other 'similar' objects.

The results of the litter experiments are summarized in
Table 4. In both cases, the regression constants are not
significantly different to those obtained in the control, with
the exception of the litter I treatment with adult Crangonyx.
Other than this, there is no indication that a litter substrate

Figure 4. The relationship between the number of Crangonyx
   captured in different habitats, after 50 minutes exposure
   to trout predation, and their initial density per 0.42 m^2.
   (A) closed circles represent the control situation, and
   the open circles litter I. (B) the litter II treatment,
   the closed circles indicate experiments conducted with
   adult Crangonyx (8.1 mm in length) and the open circles,
   juvenile Crangonyx (4.6 mm). (C) the fine litter series.
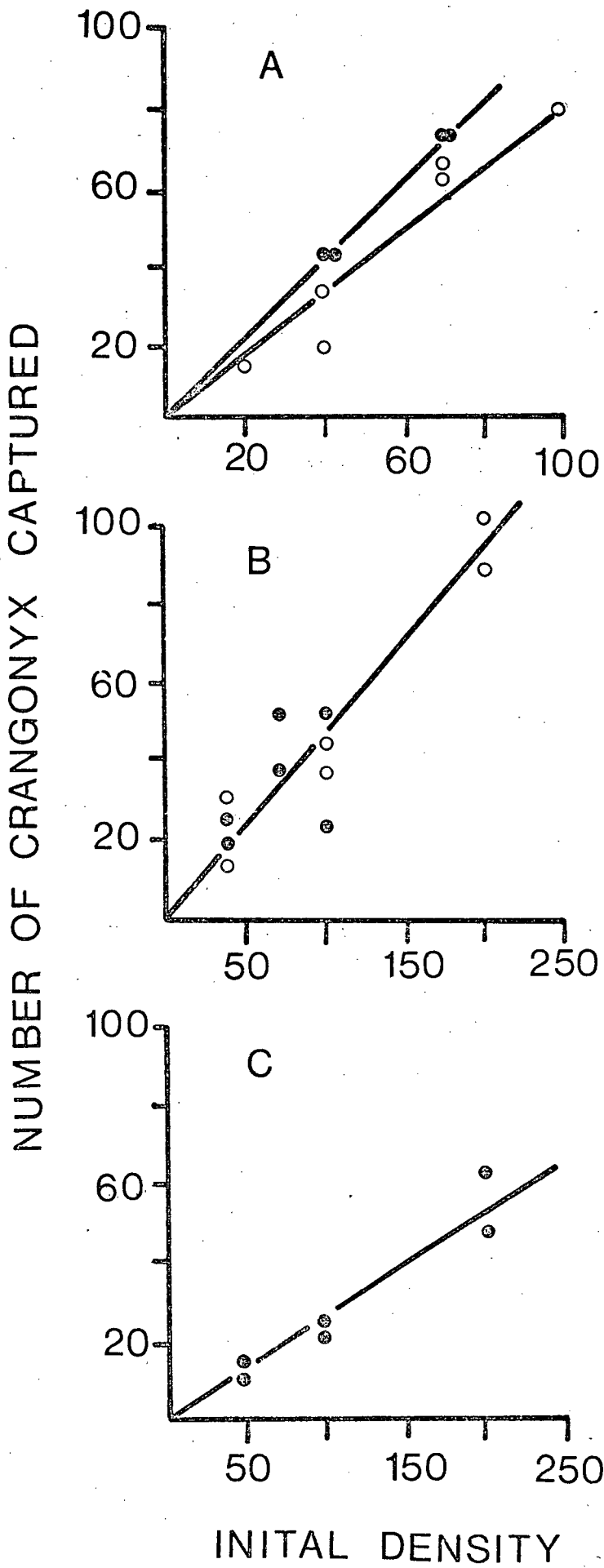
Figure 5. The relationship between the number of <u>Hyalella</u>
captured in different habitats after 50 minutes exposure
to trout, and their initial density per 0.42 m^2. (A)
the control (B) the litter I treatment (C) the litter
II treatment and (D) the fine litter treatment.
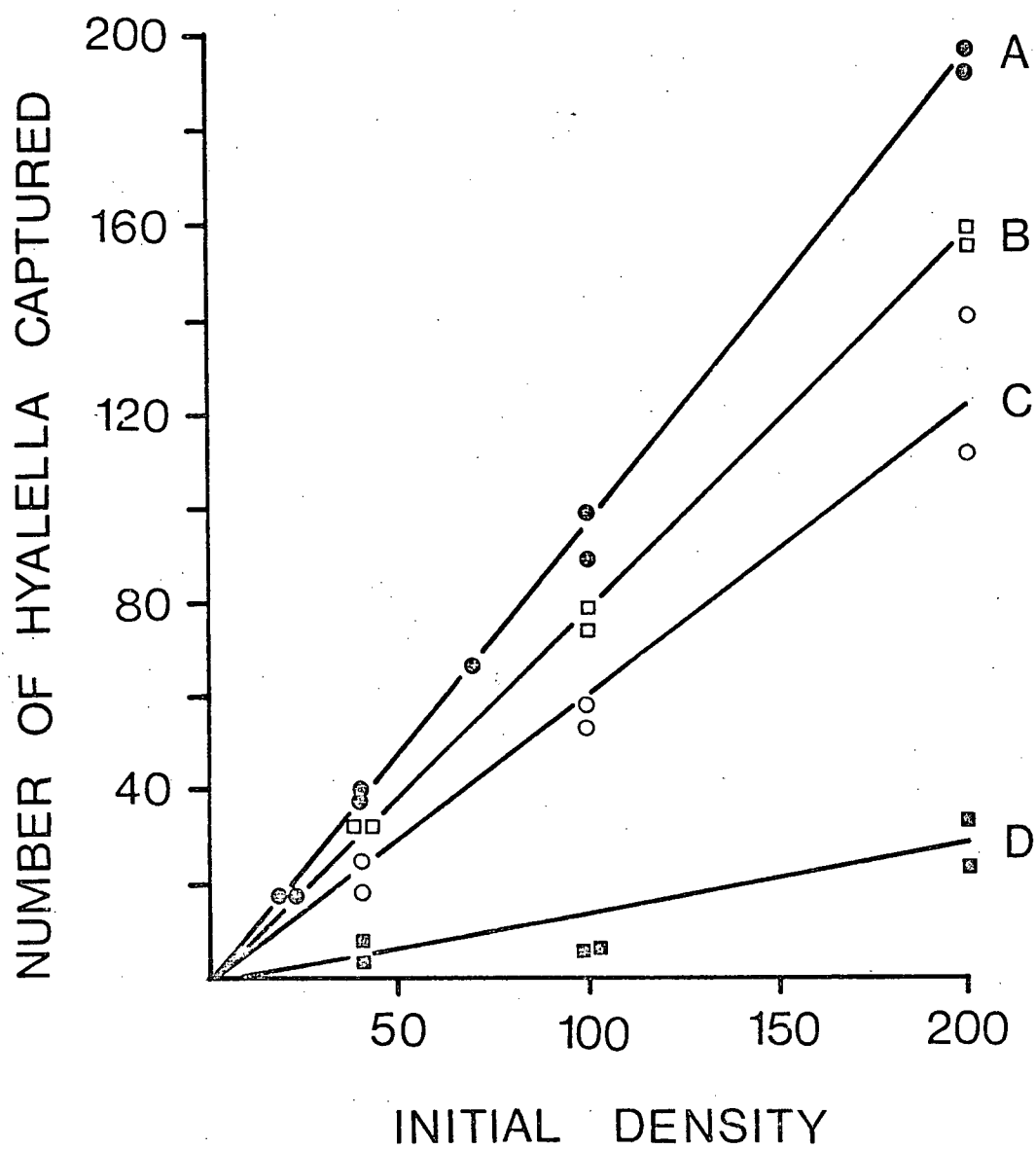
TABLE 6. A comparison of the effect of the different substrate treatments on the proportion of Crangonyx and Hyalella that were exposed and subsequently captured during an experiment. (n) indicates the number of experiments; (r) the correlation coefficient; (PE) is the slope, or proportion of prey that were captured. In part A, treatment slopes that are not bracketed by the same vertical line are significantly different at the 0.05 level or less. (V_b) is the variance of the slope. In part B, (t) is student's t.

A. Vulnerability within species

Hyalella

Substrate Treatment	n	r	Vb	PE
Control	9	0.99	.0010	0.98
Litter I	6	0.99	.0003	0.79
Litter II	6	0.98	.0050	0.66
Fine litter	6	0.90	.0014	0.16

Crangonyx

	n	r	Vb	PE
Control	4	1.00	.0000	1.00
Litter I	6	0.97	.0133	0.90
Litter II	12	0.91	.0040	0.43
Fine Litter	6	0.97	.0016	0.31

B. Vulnerability between species

	n	t
Control	13	— a
Litter I	12	1.069a
Litter II	18	24.350b
Fine litter	12	2.710b

a Not significant
b Significant at or less than 0.05 level

altered the behaviour of the trout. The concealment behaviour of the prey was the primary factor that determined the number of animals that were captured. Therefore, the relationship between the substrate, the vulnerable density of amphipods and the rate of attack can be described by modifying equation (2) as follows:

$$(3) \quad RA = b_1 \quad (PD) \quad (PE) \quad + \quad b_2 \quad (H_t) \quad + \quad K$$

where (PE) is the proportion of the population exposed (Table 6A).

The effect of prey size on the attack rate was also evident in the litter experiments. Regardless of the type of substrate, adult Crangonyx were attacked considerably faster than either juvenile Crangonyx or Hyalella. I mentioned earlier that the explanation for this observation could be due to the relationship between prey size and reactive distance. The additional piece of information that is consistent with this supposition is that Hyalella and juvenile Crangonyx are both about the same size and were attacked at identical rates (Table 4).

PREY CAPTURE SUCCESS

The success predators have in capturing food depends upon
three basic components, namely, their ability to recognize,
approach and strike at prey (Holling, 1966). Trout are not
completely successful in discriminating between prey and other
'similar' targets; they will attack inanimate objects. This
not only indicates that visual cues other than movement will
induce trout to attack but also suggests that they could 'waste'
a substantial amount of searching time if they attacked many
inanimate objects. In the litter I and II experiments, the fish
attacked relatively few pieces of litter. This was not the case,
however, in the fine litter treatment as only about 27% of their
attacks were directed toward prey; the rest were directed at
pieces of litter about the same size and color as amphipods.
Although this demonstrates that the diversity of a substrate can
influence the capture success of trout, by imparing their ability
to successfully discriminate food, this aspect is far beyond
the scope of this paper and will be treated in more detail in
another section (IV).

Once trout recognize a prey (orient toward it) they are
always completely successful in approaching to within striking
distance. Every strike they attempt, however, is not perfectly
executed as some fail to capture prey. Table 7 indicates the
strike efficiency of trout in the experiments in which this
could be determined. The results of an additional set of control
experiments, in which the prey were 11 mm adult _Crangonyx_, are

also presented.

These data (Table 7) show that regardless of the type of substrate trout were extremely successful in capturing amphipods. Since strike success (CS) was the major factor that determined if a prey would be captured, the rate of capture (RC) in the different treatments can be described simply by treating this component as a constant and adding it to equation (3) as follows:

$$(4) \quad RC = \left[b_1 \, (PD) \, (PE) \; + \; b_2 \, (H_t) \; + \; K \right] CS$$

At this point, the effects of prey size, prey density, substrate complexity and capture success have been incorporated into a single regression equation which describes the rate at which trout, in different states of hunger, can capture food. This description however, is restricted by the assumption of linearity, which implies that there is no limit to the rate of capture. This assumption, of course, is not true and is refuted by the data presented in Figure 6. In this example, the rate of capture in the first 30 seconds of the control, litter I and litter II experiments is plotted as a function of the density of exposed prey. There is little question that the capture rate approached a maximum value (average = 0.67) as the density of prey approached about 240/ sq. m. (100 amphipods in the tank). Therefore, the implicit restriction of equation (4) is that the rate of capture cannot surpass this limit regardless of the density of prey, their size, or the predator's state of hunger.

TABLE 7. The proportion of the total number of strikes which successfully terminated with the capture of prey. (N) indicates the number of experiments.

Species	Average Length (mm)	N	Mean strike success	95% confidence interval of mean
		Control		
Hyalella	5.7	7	0.907	0.812 - 1.000
Crangonyx	8.1	5	0.909	0.778 - 1.000
Crangonyx	10.8	9	0.902	0.837 - 0.967
		Litter I		
Hyalella	5.7	6	0.882	0.753 - 1.000
Crangonyx	8.1	6	0.886	0.716 - 1.000
		Litter II		
Hyalella	5.7	6	0.820	0.656 - 0.984
Crangonyx	4.6	6	0.833	0.669 - 0.997
Crangonyx	8.1	6	0.864	0.716 - 1.000

Figure 6. The relationship between the density of exposed
   prey and the attack rate. The rate of attack was
   determined over a 30 second time period. In each case,
   the predator's level of hunger was maximal with respect
   to equation (1). The data points were obtained from
   the control, litter I and litter 2 experiments with
   both Crangonyx and Hyalella.
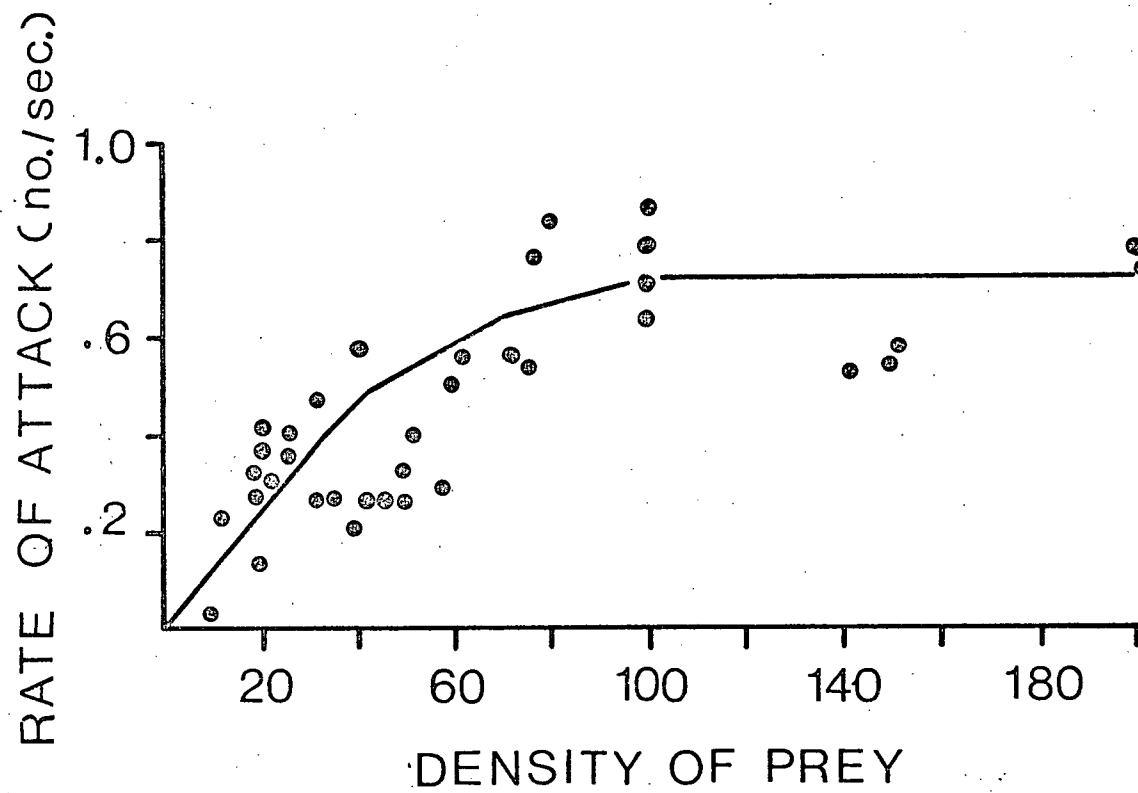
THE THRESHOLD RATE OF PREY CAPTURE AND THE SEARCHING PATTERN

Searching behaviour will decrease rapidly once an animal's hunger motivation is satiated (Beukema, 1968; Holling, 1966). Other factors however, might alter both the duration and nature of searching before this occurs.

When a trout was released at the start of a feeding experiment it would immediately move to the bottom, adopt its characteristic searching position, and begin hunting for amphipods. Figure 7 diagramatically illustrates the pattern of benthic searching behaviour during a typical experiment. As indicated, irrespective of the density of exposed prey the predator would devote all of its attention for some time to hunting for amphipods. Eventually however, this attention was disrupted and began to wane. During this phase of the experiment the fish would shift its searching position and move higher up into the water column to hunt for food, or else hold a stationary position for a few minutes. In either case it devoted less time to hunting the substrate for prey. Although in every situation the initial searching pattern was disrupted before the experiment was terminated, the duration of this phase was related to the number of vulnerable prey. The trout shifted their attention sooner when the density of prey was low. This poses the question then as to the mechanism which might be responsible for causing a predator to disrupt one searching pattern and switch its attention to another pattern (i.e. hunting for prey in the water column) or behaviour.

It seems tenable that an animal would search as long as this behaviour was reinforced but that it would shift its attention to other forms of hunting or behaviours if the rate of food intake fell toward zero. Perhaps there is a threshold rate of capture that trout must exceed if they are to continue hunting for benthic prey. If they cannot attain this threshold then they will alter their behaviour.

This hypothesis can be tested by determining if the rate of capture, when the trout first disrupted their search for amphipods, was relatively constant (threshold) irrespective of the predator's state of hunger or the type of prey it was feeding on. These data from the experiments with adult Crangonyx and Hyalella, are presented in Figure 8.

When Hyalella were prey, the capture threshold was reasonably constant (mean = 0.058 $\pm$ 1 S.E. .008) irrespective of the trout's degree of hunger. This was not true however, when the fish were exposed to adult Crangonyx; in this case, there was a significant positive relationship ($P = 0.04$) between the threshold and hunger. Nevertheless, in either instance once the rate of food intake fell below an average of 0.051 captures per second the trout moved away from the bottom of the tank. This indicates that there is a critical rate of capture although the threshold may be modified by hunger.

Once the initial searching pattern was disrupted, the fish continually changed their vertical position. They would move up into the water column for some time and then revert back to

Figure 7. A schematic representation of the pattern

of benthic searching behaviour by trout during an

experiment. (CSP) indicates the phase in which the

fish were completely attentive to hunting for

amphipods, (ISP) represents the phase in which the

benthic searching pattern waned, (PD) illustrates

the progressive decline in the density of exposed

prey, and (TRC) is the density of prey which

produces the threshold rate of capture.

% available time spent searching for amphipods
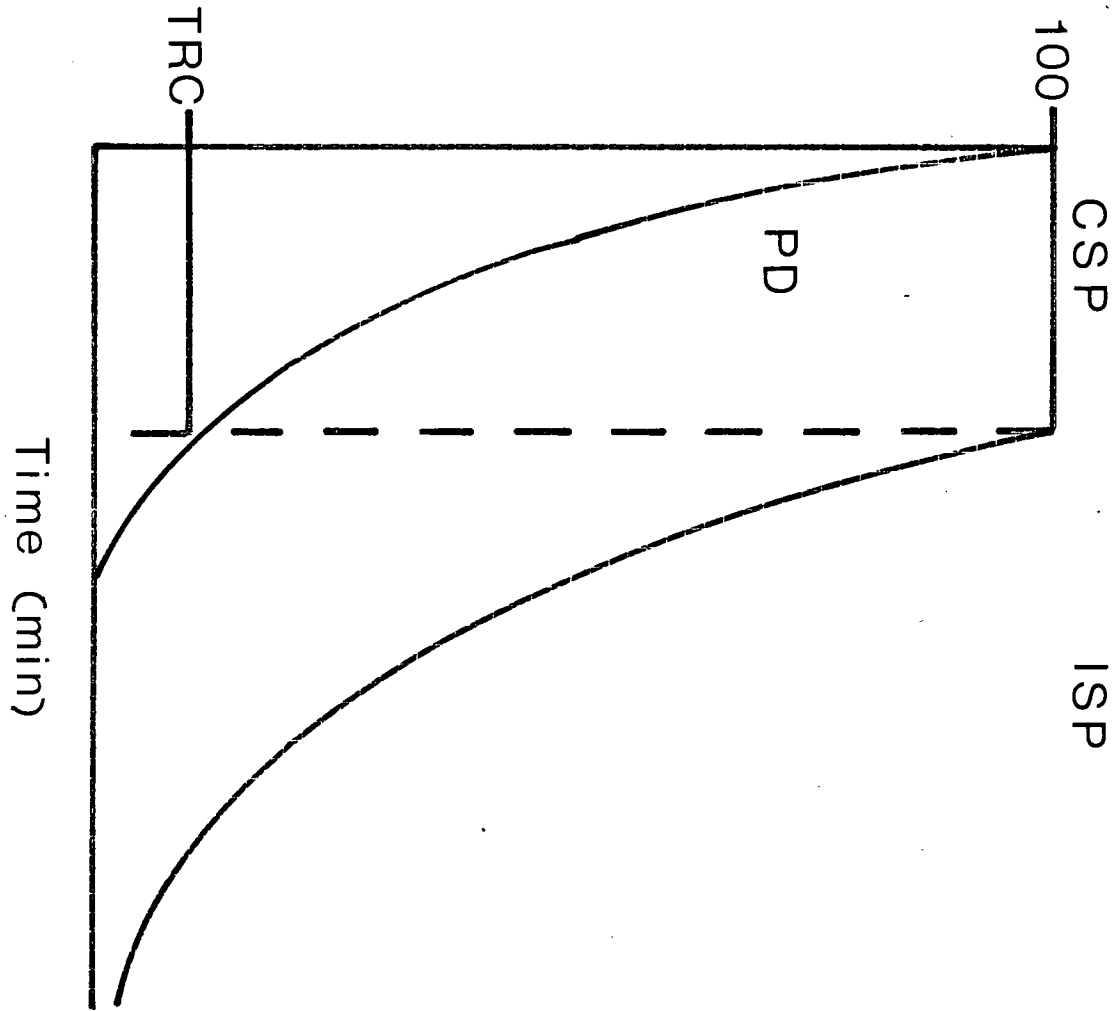
Figure 8. The relationship between the threshold rate

   of prey capture and the predator's state of hunger.

   The regression line indicated in the experiments with

   adult Crangonyx is significant at the 0.04 level.

   See text for further explanation.
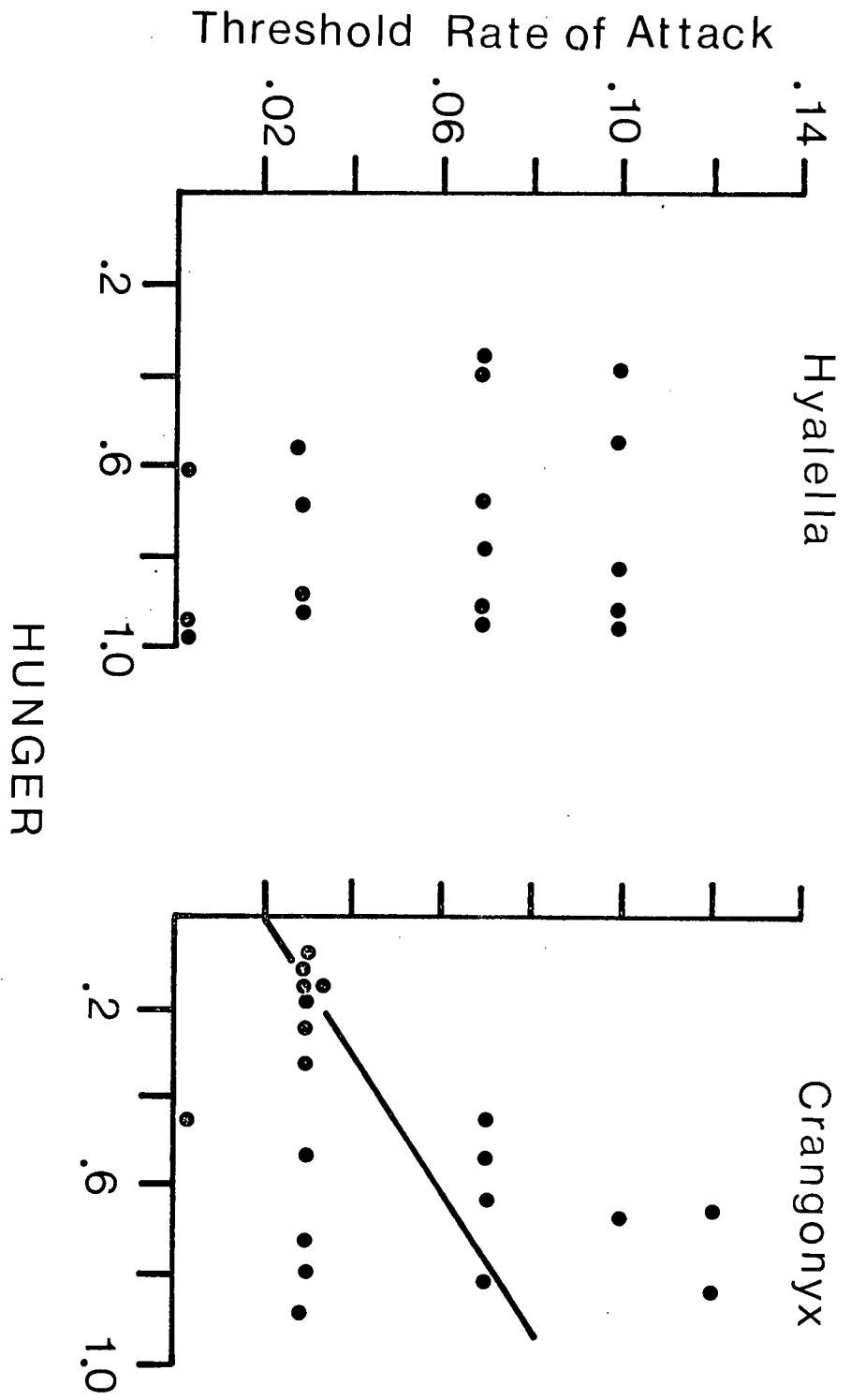
Figure 9. The relationship between the experimental

substrate and the rate of extinction of the benthic

searching pattern after the initial phase of complete

attention. Only the results obtained with <u>Hyalella</u>

are presented. The vertical bars indicate the 95%

confidence intervals of each of the means. (A)

control experiments, (B) Litter I experiments,

(C) Litter II experiments.

TIME INTERVAL (MIN) AFTER COMPLETE
ATTENTION

hunting over the substrate. Since they were no longer being reinforced for searching for amphipods, the amount of time they devoted to this behaviour waned throughout the remainder of the experiment (fig. 7).

The presence of a litter substrate did influence the feeding behaviour of the trout in one sense, however, because the rate of extinction of the benthic searching pattern was related to the complexity of the substrate (fig. 9). The trout would return to the bottom to search for food more frequently when the substrate was diversified.

DISCUSSION

Two fundamental processes, prey detection and capture will determine the food organisms which comprise an animals' food supply. The tactics a predator will utilize to locate prey will restrict not only the types of animals it can

attack but also will determine where and when it can search

effectively. If it can use more than one type of sensory

receptor to locate food it may be somewhat less restricted in

its feeding activity than predators which rely predominantly

upon vision. Ali (1959) demonstrated that salmonids, which

feed visually, could not capture prey until the ambient

illumination exceeded the rod threshold. Therefore, this

characteristic of the environment will impose restrictions

both in space and time on the feeding activity of visual

predators.

Despite this apparent drawback, there are definite advantages

to using vision to locate food. For example, it is a long

range and precise mechanism that can accurately fix the position

of a target. This is true even for fairly unsophisticated

visual systems such as those possessed by mantids and dragonfly

larvae. Although these animals can effectively detect only

moving targets (Pritchard, 1965; Rilling et al., 1959), this

is not true for predators with more developed visual receptors.

Most vertebrates can discriminate 4 visual properties of an

object; size, form, contrast, and motion (Horridge, 1968;

Prazonikova, 1969). This implies that they should be able to

detect a broader spectrum of food organisms simply because they

could effect a decision to attack on the basis of some other quality than prey movement.

Many theorists have assumed that predators will encounter food in direct proportion to the abundance of each prey organism. If this is true, then the predator must react from a fixed distance. One of the basic characteristics of any visual system is that the distance required to discriminate an object is almost proportional to the size of the target. Therefore, visual predators such as rainbow trout have the opportunity to react to large prey from a greater distance than smaller prey. It was demonstrated that the distance of reaction of trout is dependent upon prey size and that this could explain why they attacked adult Crangonyx faster than either Hyalella or juvenile Crangonyx.

The searching position that rainbow trout adopt when they hunt for benthic prey was only considered superficially in this study. This behaviour, however, has an interesting implication. A predator can only detect a prey if the height of its searching position is less than the distance it requires to release an attack. If this condition is not met then some small size classes of prey may be invulnerable to detection and subsequently, capture. There is some evidence that this inference may apply to rainbow trout (section IV).

Both of these characteristics, a reactive distance that is dependent upon prey size and a specific searching position, are basic components of the feeding behaviour of trout. These same characteristics are sufficient to explain the well documented

field observation that many species of fish disproportionately exploit large prey and frequently fail to consume others below a threshold size (Ivlev, 1961; Brooks, 1968). Ivlev (1961) also pointed out that very effective bottom feeding fish do not rely primarily upon vision to detect food and do not appear to adopt pronounced searching positions. Since other species of salmonids appear to behave similarly to rainbow trout (Schutz, 1969; Sheperd, 1970) this may explain why they tend to be relatively ineffective predators of many inconspicuous benthic-living organisms (Smith, 1961).

Capture success also affects the types of prey a predator can exploit. In the present study, there was no indication that the size of the prey considered significantly impared the capture success of trout. In theory, however, there must exist both an upper and lower limit to the size of organism that can be successfully manipulated by predators which swallow their food. Within this range, there is likely to be an optimum sized prey that can be captured most successfully. Both Holling (1964) and Dixon (1959) have demonstrated that capture success tends to diminish if the prey is either larger or small than the optimum size.

The process of predation is not only dependent upon the components of prey detection and capture success, but also the density of prey, the predator's hunger motivation and the degree to which learning can alter the behaviour of either the predator or prey. Holling (1966) has discussed the influence of prey density and hunger motivation on the functional response of

predators. The action of these components proved to be identical for trout, therefore, their significance will not be reiterated here beyond stressing that increasing prey density stimulates the attack rate while diminishing hunger motivation antagonizes this effect. The possibility that the behaviour of trout could be altered by learning will be treated later (Section II). In any case, all of these characteristics will operate to determine the rate of capture, which in turn could influence the searching pattern a predator adopts.

Although the cessation of hunger will naturally terminate searching, this behaviour is undoubtly sensitive to other signals as well. Most responses will wane if they are not reinforced intermittently; this is evident, for example, in the attack response of mantids. If they are not rewarded for striking at a 'dummy' target they will simply stop responding (Rilling et al, 1959; Holling, 1966). The searching behaviour of trout is completely analagous because if they are not sufficiently reinforced (threshold rate of capture) they will shift their pattern of search. This feedback has been suggested to be responsible for the changes in the feeding position of trout in mountain streams (Jenkins, 1969).

This same feedback also suggests that trout could temporarily converge into areas in which prey are relatively more vulnerable to attack. By simply randomly shifting their position, some individuals will locate areas of prey abundance. If the density of prey is high enough to surpass the threshold

rate of capture, then the predator may remain feeding in the area. Given enough time, most of the population could converge into a specific region or at least adopt the same relative searching pattern,such as feeding in the water column or over a substrate.

The phenomenon of convergence has been reported for other animals (Neish, 1970; Tinbergen, 1960) as well as . fish (Allen, 1941). Holling(1959a) pointed out that predators that can invoke an immediate numerical response, such as converging, will function as a stabilizing component of the community because they will tend to counteract any serious imbalance in prey abundance.

In conclusion, the observation that trout will shift their pattern of search if they are not being sufficiently reinforced implies that the population will disperse through the water column and will tend to converge temporarily into areas in which prey are relatively more vulnerable to attack. In addition, since trout were found to react to only exposed prey and displayed an attack response that was dependent upon prey size, this . suggests that they should be effective predators of large, exposed animals but would be relatively ineffective in capturing smaller or more cryptic species.

SUMMARY

1) In experiments without a litter substrate, it was shown that both prey density and the hunger motivation of trout affect their rate of attack. These two components are antagonistic

since the former increases the attack rate while the latter depresses it.

2)   The reactive distance of rainbow trout is dependent upon prey size. This could explain why they attacked adult Crangonyx, the largest prey, faster than either Hyalella or juvenile Crangonyx.

3)   When a substrate was present, both species of prey concealed themselves. The proportion that were exposed was inversely related to the amount of cover area. Since trout will detect only exposed prey, their attack rate was inversely related to the diversity of the substrate.

4)   There was no consistent indication that the presence of a substrate directly altered the feeding behaviour of trout. The concealment behaviour of the prey was the primary factor that determined the outcome of the litter experiments.

5)   The ability of rainbow trout to capture prey was shown to be independent of both the size of the test prey and the diversity of the substrate. The latter however, did impare their success in discriminating amphipods.

6)   In the laboratory, trout must be reinforced at a rate that exceeds 0.051 captures per second if they are to maintain

a specific searching pattern. If they do not attain this
threshold they will switch their attention to other hunting
patterns or behaviours. Once this occurs, the original pattern
will wane at a rate that is inversely dependent upon the diversity
of the substrate.

7)   Due to 4 major characteristics of their feeding behaviour:

     i)   the dependence of the reactive distance on
         prey size,

    ii)   the searching position,

   iii)   the fact that they will attack only exposed prey,
         and

    iv)   the threshold rate of capture

rainbow trout are likely to converge into areas in which prey
are relatively abundant, should be effective predators of large,
exposed prey; but should be considerably less effective in
exploiting smaller or less conspicuous species.

SECTION II

THE EFFECT OF EXPERIENCE ON THE RESPONSE
OF TROUT TO UNFAMILIAR PREY

INTRODUCTION

The concept of the "searching image" has attracted
considerable attention in the fields of animal behaviour and
ecology since it was first proposed by Tinbergen (1960). He
and others since then, have suggested that many animals can
learn to increase their responsiveness to prey, but that, if
they are not continually reinforced they will shift their
attention to other objects. Both of these features would be
adaptive since they would enable predators to hunt with "maximum
efficiency" (Croze, 1970). The existence of this behaviour
has been demonstrated by experimental studies on various
vertebrates (Beukema, 1968; De Ruiter, 1952; Holling, 1959a;
Croze, 1970).

To date, the aim of most of this work has been to reveal
the components of feeding behaviour that appear to be affected
by learning and to examine the resulting ecological implications.
With these considerations in mind, Holling (1965) developed a
general model to account for the learning process. He suggested
that experience operated through a system of feedbacks between
the palatability of prey and the predator's state of hunger to
affect the distance of its reaction to prey. Simulation studies
demonstrated that the model was sufficient to account for the
phenomenon of the searching image and had important implications

with respect to the selective advantages of mimicy between palatable and less palatable prey.

The experiments described in this section were designed to examine some of the factors which might influence the response of rainbow trout to artificial, but palatable prey, and to determine if associative learning could be an important component of their behaviour. The results were then interpreted in terms of Holling's model to test if it was sufficiently general to account for the effect of learning on the feeding behaviour of trout.

METHODS AND MATERIALS

The rainbow trout selected for this study ranged in length from 11 to 14 cm (1 to 2 years old) and were obtained from Marion Lake, British Columbia. To insure that the fish were completely naive, the experimental prey were formed from commercial chicken liver. The shape and size of the prey were standardized by cutting cylindrical pieces of liver 3 mm by 5 mm in length.

Conditioning experiments were conducted in two entirely different situations. In the first set of experiments (A), individual naive fish were placed into a small holding chamber (30 x 12 x 20 cm) that was suspended in a 50 gallon (227 liter) glass aquarium. Six standard prey were then scattered at random through the tank. After the food had been introduced the trout

was released from the holding area. An experiment lasted for

20 minutes and was considered to represent one 'day' of experience

regardless of whether the animal fed or not. Experiments

were conducted every 48 hours until the amount of time the fish

required to locate and capture all 6 prey stabilized. Between

successive experiments the predators were held in isolation and

without food.

All other experiments (B) were conducted in a large rectangular

tank (180 x 16 x 30 cm) which had a small holding area at one

end. This chamber was separated from the remainder of the tank

by an opaque, sliding partition. One side of the tank was

marked off in 1 cm intervals so that the distance from which

trout would react to prey could be estimated.

For each feeding experience a fish was transferred to

the holding chamber in the experimental tank. Before the

predator was released a single prey was placed near the opposite

end of the tank. The reactive distance was defined as the

distance between the predator and prey when the fish attacked.

After a prey had been captured, the trout was returned to the

holding chamber while another piece of food was introduced. A

single day of experience consisted of six successive captures.

Once these were complete, the predator was returned to its

holding tank and deprived of food until the next test period

48 hours later.

In some (B) experiments the trout were exposed to prey

that contrasted differently with the background. The level of

target contrast was changed by staining the standard white prey in a saturated solution of Sudan Black B. Several different degrees of contrast (light grey to black) could be reproduced by varying the length of the staining time. Although the term, contrast, is commonly defined as the difference in the amount of light reflected by a target with respect to the backround (le Grand, 1967), it is used in a relative sense throughout this paper. In other words, in both sets of experiments, the standard white prey had a high contrast relative to either the dark grey or black prey because the background (tank bottom) was black.

In both sets of experiments, the water temperature (10 $\pm$ 2 C.) the background (tank bottom) illumination (0.3, ft-candles) and the turbidity of the water (attenuation coefficient, 0.50) were carefully controlled to insure that the visual acuity of the fish was not affected by changes in any of these conditions.

RESULTS

EXPERIMENT A

THE CHARACTERISTICS OF THE INITIAL RESPONSE OF TROUT TO UNFAMILIAR PREY

When trout are exposed to unfamiliar prey several aspects of their feeding behaviour change with experience. Although some fish will investigate an unfamiliar stimulus the first time they experience it, others require repeated exposure before they will react. The number of successive exposures an individual required before it would attack was defined as the latent phase. The average duration of this phase for a group of 9 test fish

was 4 days and ranged from 1 to as high as 11.

Once the latent period was terminated, the behaviour of the fish continued to change as they acquired further experience. Four separate steps preceed their capture of prey: 1) orientation, 2) fixation, 3) attack, and 4) strike. Once the fish began to react to the test prey many individuals would fail to complete an attack sequence. Some animals would visually fixate prey and then fail to follow through with an attack, or attack, but fail to capture prey. The duration of this phase was found to average two further days of experience after the termination of the latent period. Although trout will apparently develop a complete attack sequence rapidly if a prey is palatable this may not be true if it is relatively unpalatable (Sheperd, 1970).

After the trout established a complete attack pattern, the amount of time they took to capture all 6 prey diminished as they became more familiar with them (fig. 1). Evidently, some other component of their behaviour was still changing after 6 days of exposure. Holling (1966) demonstrated that the attack rate is determined primarily by three factors: 1) the density of prey, 2) the relative velocity between the predator and prey, and 3) the predator's distance of reaction. In the present experiments experience could have affected either the velocity of the fish or their reactive distance. On the basis of observation, it did not appear as if their velocity changed considerably from one experiment to the next. Therefore,

Figure. 1. The effect of experience on the feeding time

and reactive distance of 2 groups of trout. The open

circles indicate the average amount of time it took 9

fish to capture 6 standard (white) test prey; the

range is presented. The closed circles show the

average change in the reactive distance of 6 different

trout. Further explanation is given in the text.
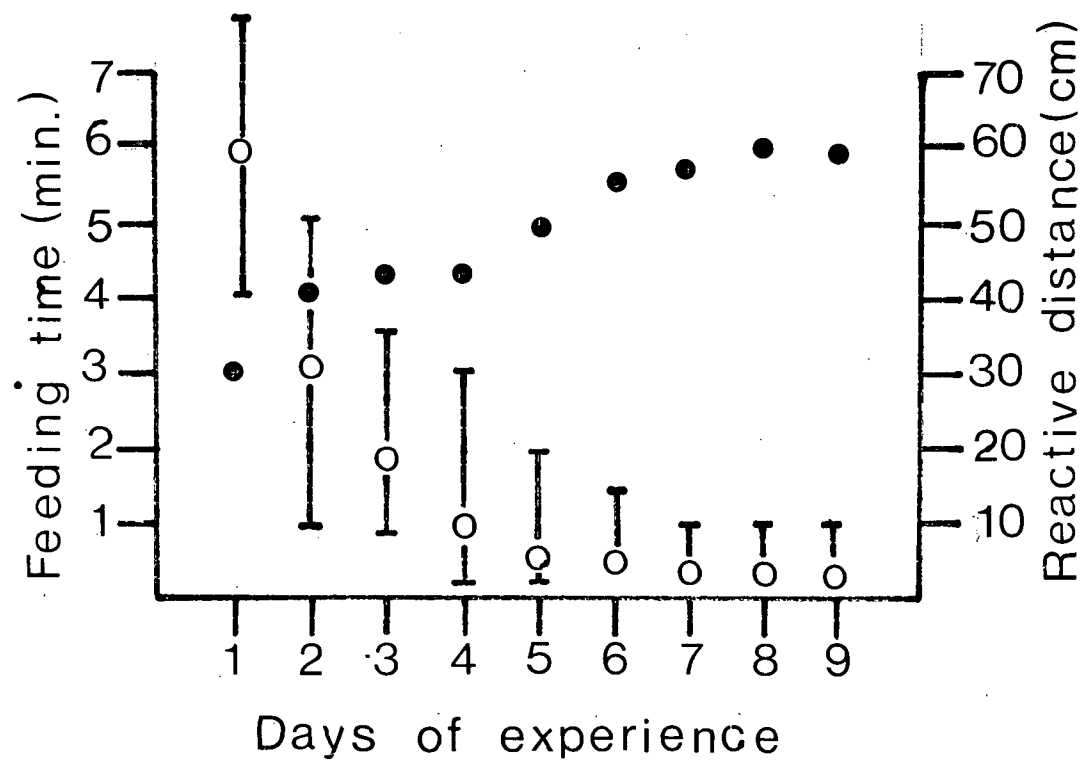
the effect of experience on their reactive distance was examined.

EXPERIMENT B

THE EFFECT OF EXPERIENCE ON REACTIVE DISTANCE

In these experiments 6 naive trout were exposed to standard
prey in the rectangular tank. After this group passed through
the latent phase, their reactive distance was recorded for up
to 16 consecutive days of experience. The results indicated
that the intitial reactive distance of every individual increased
with further experience before it finally stabilized at a
considerably higher level (fig. 2). In most cases the trout
required 6 to 7 days of experience (about 40 exposures to prey)
to develop a maximum reactive distance. One animal (4) however,
required somewhat more time. Both of these aspects, the initial
attack distance and the time required to develop a response,
indicate that the process of learning can vary considerably
between individuals.

Nevertheless, if these data are pooled and averaged, it
is apparent that the change in reactive distance of the second
group of fish is inversely correlated with the duration of the
feeding period that was required by the first group (fig. 1).
This suggests that as the fish acquired experience, an increase
in their distance of reaction could have been the causal
factor behind the increase in their rate of attack (decrease
in feeding time).

In the process of learning the first few experiences trout have with new prey are likely to have the greatest effect on their response. This hypothesis can be expressed as:

$$\frac{d\ RD}{d\ E} = a\ (RD_{max} - RD)$$

where (RD) is the distance of reaction for a given level of experience (E), (a) is a rate constant and (RD_{max}) is the maximum distance from which a conditioned animal will attack. This expression integrates to,

$$(1) \quad RD = RD_{max}\ (1 - e^{-a\ (E)})$$

The average value of (RD_{max}) was calculated by pooling all the data in Figure 2 for the last day of experience (Table 1). Once this parameter is known, the value of (a) can be estimated by standard regression techniques if (1) is first linearized by a logarithmic transformation. A regression analysis was conducted by grouping all the data in Figure 2. The results showed that if these data were transformed they could be described adequately by a straight line (r = 0.90) but that the line did not pass through the origin. Therefore equation (1) was modified to include an intercept (b). The value of (a) and (b) are presented in Table 1.

In most cases, the trout were able to double their initial

Figure 2. The effect of experience on the reactive distance
of 6 trout. The test prey were 'white' (5 mm in length).
Each data point represents a mean of 6 replicate observations,
the range is indicated for several days of experience.
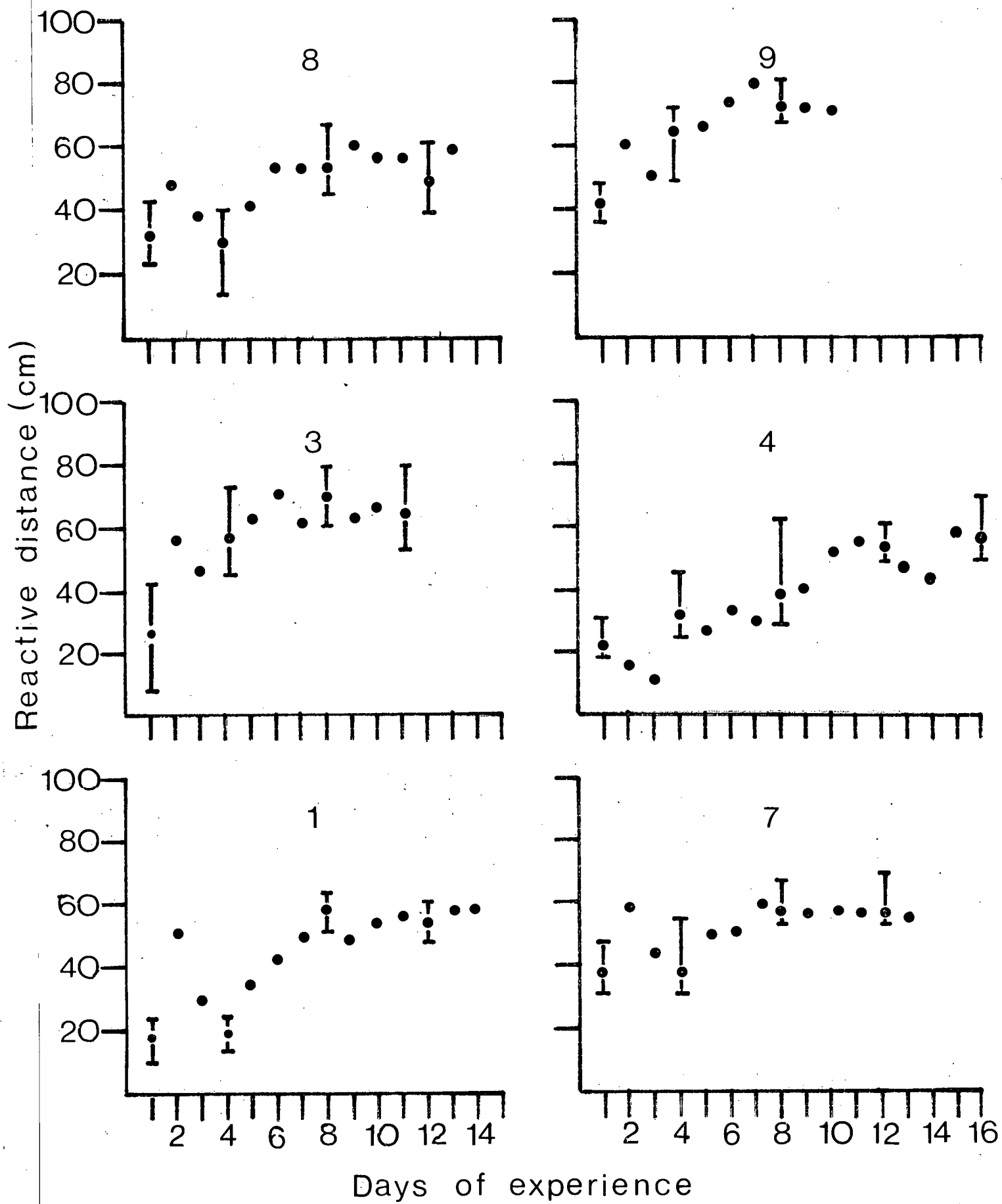
TABLE 1. The relationship between the initial (RDT) and conditioned reactive distance (RD_{max}). The simulated prey were 'white' (high contrast) and 5 mm in length. The average values of (K), (a) and (b) were obtained by pooling all the data. Further explanation is given in the text.

Fish	RDT (cm)	RD_{max} (cm)	K
1	20	56	2.8
3	26	64	2.5
4	24	56	2.3
7	36	58	1.6
8	32	56	1.8
9	40	74	1.8

Average Parameter Values

RDT	=	29
RD_{max}	=	61
K	=	2.0
a	=	0.466
b	=	- 0.038

naive reactive distance after 6 days of experience. If the maximum distance from which a conditioned animal will react is assumed to be a constant function (K) of its initial response (RDT) (Table 1) then the relationship between these two parameters is simply:

$$(2) \quad RD_{max} = K \text{ (RDT)}$$

By substituting equation (2) into (1), the effect of experience can be expressed in terms of an animal's naive response rather than its maximum reactive distance. The result is,

$$(3) \quad RD = K \text{ (RDT)} \left(1 - e^{-a(E) + b} \right)$$

THE SPECIFICITY OF THE ATTACK RESPONSE OF CONDITIONED TROUT

Since trout can increase their reactive distance through learning, the question which arises is just how specific is their response to a prey? Most vertebrate and some invertebrate visual systems receive at least 4 distinct pieces of information about any object: 1) size, 2) form, 3) contrast and 4) velocity. Therefore a target is not just one stimulus but rather is a composite set of at least these 4 visual properties. Undoubtly, an animal could use several if not all of these cues to form a learned association. Some cues however, might be more important than others.

To answer this question, I decided to condition trout to standard white prey and then switch them to another object with identical physical properties except for contrast. If the response of a conditioned animal is not specific then its reaction to a 'new' object should not change with experience.

However, since I choose to alter the level of prey contrast to test for the specificity of the attack response, another variable must be taken into consideration.

Hester (1968) as well as others have documented that a visual animal must detect a threshold level of contrast before it can discriminate an object from the background. Underwater, the contrast of a target will appear to attenuate as one moves further away from it. As a result, if an object has a high level of contrast it can be detected from a greater distance than one with less contrast. Consequently, if trout are conditioned to a white target and then switched to one with lower contrast (i.e. black prey) their maximum distance of reaction should be different. The white prey should be attacked from a greater distance. This does not indicate response specificity but is predictable on the basis of visual mechanics. The question is, however, will the reaction of trout, conditioned to one target (i.e. white), change as they acquire experience with a 'new' prey. If their response is not specific then they should react to the 'new' object from a "maximum distance" on the first day; if their response is specific, then their distance of reaction should improve with experience. In either case, if

the contrast of the 'new' prey is lower than the original then the maximum reactive distance should be less.

Nine trout were conditioned to standard white prey until their reactive distance stabilized for 4 successive days of experience. They were then assigned, at random, to be switched to either a light grey, dark grey, or black prey. Two fish were assigned to each type of prey, with the exception that 4 fish were transferred to black prey. The remaining animal served as a control (white).

On the first day of exposure the fish transferred to the light and dark grey prey reacted immediately. Their response did not change as they acquired additional experience, they attacked without hesitation and from a maximum distance (figs. 3B, 3C). For the trout exposed to dark grey prey, however, the effect of target contrast was apparent because their average distance of reaction was considerably less than the control (fig. 3A).

There was a noticeable change in the behaviour of the trout exposed to black prey. On the first day every individual had to be released from the holding area an average of 20 times before it would react. This lag interval corresponds to the original latent period, although in this case, it was not as pronounced. Part of the explanation may be due to the fact that the experimental environment was extremely simple and that the 'new' prey retained many of the physical characteristics of the original object. The second and by far the most pronounced change in behaviour was in the reactive distance

page 60 omitted
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component. These data are shown in Figure 3D and clearly indicate
that the attack distance increased significantly as the fish
acquired more experience.

The behaviour of the fish transferred to black prey can
be summarized by saying that they initially appear to be
'searching for something else'. Once they began to respond to
the new prey, however, they were able to increase their distance
of reaction which demonstrates that they were not treating
every object in the tank identically. Their conditioned response,
therefore, was somewhat specific.

The hypothesis that both the rate of learning (a) and the
level of the conditioned response (K) are independent of contrast
can be tested with the data presented in Figure 3D. Using the
estimates of (K), (a) and (b) from previous experiments (Table
1), and the initial distance from which trout attacked black
prey (RDT) as a starting point, the change in their response was
predicted from equation (3). Since there is a reasonably close
fit between the observed and predicted trend (curve, fig. 3D),
this demonstrates that the rate of learning was not affected by
prey contrast.

To summarize, these experiments demonstrate three points:
1) the response of conditioned trout is somewhat specific, 2)
the maximum distance trout will react to prey is dependent upon
target contrast, and 3) prey contrast does not affect the rate
of learning.

Figure 3.   The effect of switching trout, conditioned to

white prey, to prey with different levels of contrast.

The data points indicate the mean reactive distance of

each group.   The 95% confidence limits of each mean on

the first and last day of experience are shown.

(A) white prey (control), (B) light grey prey, (C) dark

grey prey, (D) black prey.

Days of experience
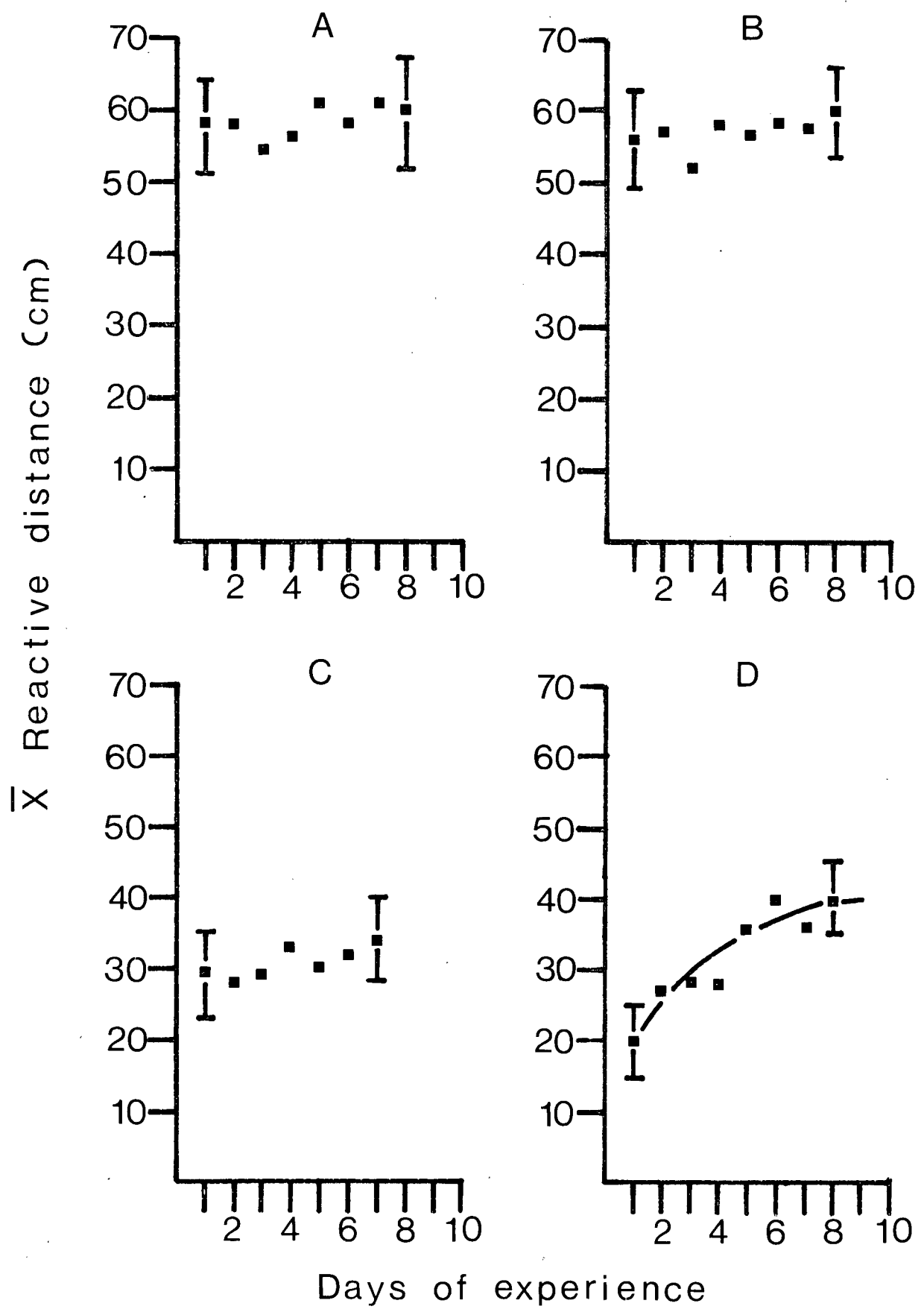
THE EXTINCTION AND RE-DEVELOPMENT OF REACTIVE
DISTANCE

To examine the effect of long-term deprivation of reinforcement on reactive distance, the 4 fish previously conditioned to black prey (fig. 3D) were deprived of further experience for 90 days. During this period they were fed standard white prey. Upon re-exposure to black prey their reactive distance was recorded for several successive days. Figure 4 shows that the group's initial response after re-exposure (18 cm) was not significantly different from their response when they were naive (20 cm). In addition, they required 4 to 5 days of experience to re-develop a conditioned response which is similar to the 5 to 6 days they originally took (fig. 3D).

Although the effect of short-term deprivation of reinforcement on reactive distance was not examined in detail, one set of experiments indicated trout can maintain a maximum response for up to 14 days without reinforcement. Therefore, some period of deprivation between 14 and 90 days is sufficient to reduce the reactive distance back to the original level (RDT) when the animal was naive.

ATTENTION COMPETITION

The experiments described thus far have been concerned with the effect of experience on the distance of reaction when a predator was exposed to one type of prey. If it were faced

Figure 4.   The re-development of the reactive distance

of 4 trout.   The prey were 'black' (5 mm in length).

The data points represent the average distance of

reaction.   The 95% confidence limits of the means

are shown.   The curve was fitted by eye.
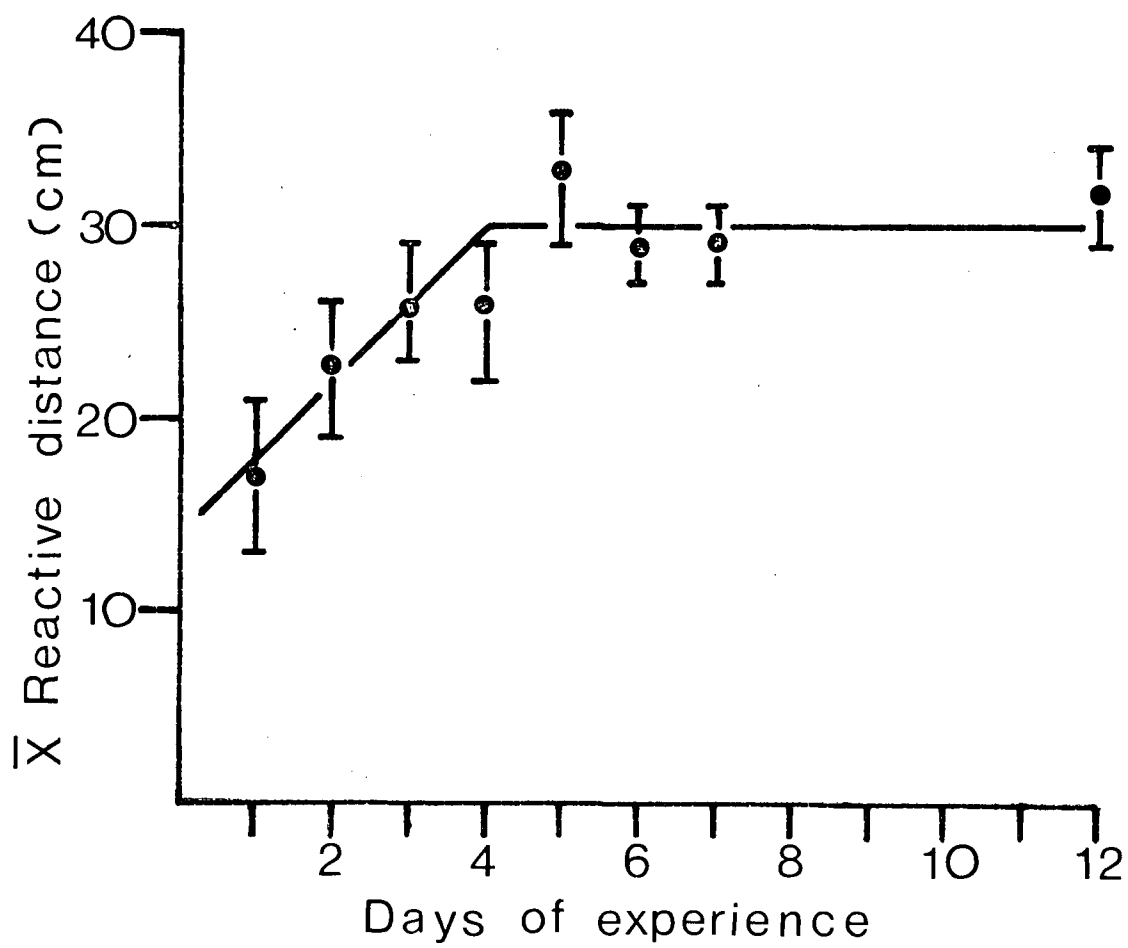
with a situation in which it could encounter other familiar
objects then some form of attention .competition, or interference
might occur. For example, the distance trout will react to
one prey might be somewhat diminished if they attempted to
become generally responsive to alternate forms.

To examine this possibility, 4 trout were conditioned to
low contrast (black) prey until their reactive distance
stabilized. They were then switched to a situation in which
each time they were released they could encounter either a black,
white or dark grey prey, with equal probability. These targets
were identical except for their contrast. Although their most
recent experience had been confined to black objects the fish
had been previously exposed to the alternate types and were
therefore somewhat familiar with them.

Before they were switched, the trout attacked black
prey from an average distance of 32 cm (n - 15; 1 S.E. $\pm$
1.0); when alternates were present, they reacted from a distance
of 37 cm (n = 16; 1 S.E. $\pm$ 2.7). This difference is not
statistically significant, therefore, it must be concluded
that the presence of alternate food did not affect the distance
of reaction.

DISCUSSION

Experience with an unfamiliar prey will alter several components of the feeding behaviour of rainbow trout: 1) the latency of their response, 2) the development of a complete attack sequence, and 3) the reactive distance. All of these aspects have some theoretical importance, the latter observation however, is by far the most significant. Beukema (1968) demonstrated that these behavioural alterations also occured when sticklebacks were exposed to a novel food and led him to infer that such changes, especially in the distance of reaction, were necessary if a predator was to develop. a searching image.

The present study demonstrates that each time a predator, which is capable of learning, attacks a palatable prey it will increase its reactive distance for that object. One critical condition must be met, however, before the attack response can develop any further. That is, another prey must be encountered before the new attack distance diminishes back to the original level. If the rate of learning is faster than the rate of response extinction then even a few contacts with a relatively rare prey could be sufficient to promote the development of a searching image. The difference between these two antagonistic rates will determine the density of prey that is required before a predator can form a searching image (maximum reactive distance).

Many prey populations tend to be polymorphic with respect

to color, form, or some other visual quality. Croze (1970)
showed that if predators discriminate between morphs then a
polymorphic population will be less vulnerable to attack than
a monomorphic population of the same density. This conclusion
however, may not be applicable when prey are extremely abundant
(Holling, 1965). In any case, over a wide range of densities
the extent to which polymorphism will decrease the risk of a
prey is affected by, among other things, the specificity of the
searching image. The risk from predation will be greatest
when the morphs are 'similar' enough to be treated identically by a
predator. On the other hand, predation will be minimized when
the predator will react to only one form. Although this will
result in maximum protection for the population, predation will
also be low if the predator does not react to each morph from
a maximum distance. In the present study, the response of
conditioned trout was shown to be somewhat specific but that
they were able to increase their responsiveness to 'new' prey
at a low level of reinforcement (6 encounters every 48 hours).
These characteristics imply that they have the potential to
learn to discover polymorphic prey that are relatively scarce.

Holling (1965) as mentioned earlier, developed a general
model of the learning process. One of the assumptions of the
model is that pathways of associative learning do not interact
but are formed independently of existing paths. The alternative
to this is the concept of interference, in which the presence
of alternate stimuli could affect either the rate of development
of new pathways of learning or the performance of already
existing ones. Interference is supported by some data for

humans.   Shiffrin (1970) reported that the probability

that an individual would recall a particular item was inversely

related to the number of elements associated with the task.

Attention competition, which is but one possible form of

interference, could not be demonstrated for trout nor for

sticklebacks (Beukema, 1968). Under the experimental conditions,

however, both animals had to recognize only 2 or 3 types of

prey; under more natural conditions predators will detect

both a wider variety of prey as well as conflicting stimuli

from the environment. Thus the possibility of interference

is increased.

The learning model proposed by Holling also assumed that

the hunger level of a predator determined whether it would attack

or ignore any prey it encountered. For an attack to occur, the

predator must be hungrier than the attack threshold it has set

for that prey. Learning operates by raising or lowering the

attack threshold from some initial general level. If the prey

is palatable, then the attack threshold is lowered with each

successive encounter; if it is unpalatable, then the threshold

is raised. Since the reactive distance is postulated to be

functionally dependent upon the predator's state of hunger

the shift in this threshold is overtly expressed by a change

in reactive distance.

The relationship between the palatability of prey and the

attack threshold of trout was not examined. However, there is

considerable evidence to indicate that the amount of food many

fish will ingest is dependent upon its palatability. Both

Sheperd (1970) and Ishiwata (1968e) have shown that fish consume considerably less unpalatable food before they voluntarily cease feeding. Hence, there is little doubt that the attack threshold of many animals is related palatability. On the other hand, the relationship between hunger and reactive distance has not been adequately documented for many predatory species.

Even though Holling's model will predict that the distance of reaction should increase as trout acquire more experience with palatable prey there is some question as to the generality of the mechanism through which learning is proposed to operate. Beukema (1968) presented some evidence which implied that the reactive distance of conditioned sticklebacks was stable over a wide range of hunger levels. I also have some preliminary data which suggests that short term changes in the amount of food trout have ingested does not change their responsiveness (Table 2). Although neither of these studies are sufficiently detailed to allow rejection of the hypothesis that hunger affects the distance from which all predators will react, the data do lead one to suggest that the effect of hunger on reactive distance should be carefully examined. If the proposed relationship cannot be demonstrated then the learning model must be modified to incorporate an alternate pathway in which experience directly affects a predator's responsiveness, rather than indirectly through its hunger motivation.

Irrespective of the mechanism of learning, it was shown that trout can double their attack distance if they acquire

sufficient experience. Therefore, if certain conditions prevail
they have the potential to selectively exploit prey. This
inference is supported by several field studies (Allen, 1941;
Hamilton, unpublished data; Bryan, personal communication)
which found that individual salmonids often contain just 2 or
3 main food organisms in their gut in conjunction with a number
of alternate prey. This phenomenon could be explained to some
degree if predators restricted their hunting activities to
specific sectors of the environment. However, this does not
appear to be a complete explanation since animals in the same
relative area will often feed on different organisms. This
is not suprising, because variations in the experiences and
motivational levels of individual predators can be expected to
affect the rate they encounter different prey as well as the
conditions necessary to promote learning.

In conclusion, the changes in the feeding behaviour of
trout, as they acquire experience, reflect many of the characteristic
of the searching image reported by Croze (1970). He showed
that before crows shift their attention there is a lag phase
in which they will not react to an unfamiliar object. This
corresponds to the latent phase for trout. However, once they
discover new prey both animals display a capacity to learn quickly.
Although trout appear to require somewhat more time to become
completely responsive this is difficult to determine because
they were exposed to a different schedule of reinforcement.

Another characteristic of the searching image is that it

TABLE 2. The effect of hunger on the reactive distance of 3 trout, conditioned to 'white' prey (5 mm). The hunger index describes the proportion of the stomach that is empty. An index of 1.0 indicates that there was no food in the gut. An index of 0.5 indicates that the gut was half full. The fish were fed one hour before an experiment. (n) indicates the number of experiments

Fish	Hunger index	n	Mean reactive distance $\pm$ 1 S.E. (cm)
3	1.0	12	84 $\pm$ 3.3
3	0.5	6	94 $\pm$ 1.5
5	1.0	12	79 $\pm$ 3.6
5	0.5	6	73 $\pm$ 4.8
9	1.0	12	83 $\pm$ 3.2
9	0.5	6	90 $\pm$ 1.8

is relatively specific. This is true to some extent for trout

as well, since the group conditioned to white prey did not

react immediately when they were switched to black prey. In

this case, the latent period was not very pronounced, possibly

because the 'new' object retained many of the characteristics

of the original prey. Nevertheless these experiments indicate,

as Croze pointed out, that the searching image is specific but

can be transferred if the original image is no longer reinforced.

SECTION III

PREY ACTIVITY AND VULNERABILITY

INTRODUCTION

The experiments described in Section I showed that trout
only attack exposed prey. Therefore, it is essential to
distinguish between the actual density of a prey population
and the vulnerable density.

Crangonyx richmondensis and Hyalella azteca are important
prey of the trout population in Marion Lake; both species are
burrowing amphipods and tend to spend much of the time actually
concealed within the sediment. In general, the activity of
these animals appears to be confined to the short intervals
in which they are exposed at the mud-water interface.

In this section, I will examine the effect of water temperature
on the proportion of amphipods that are exposed (vertical activity)
as well as the average amount of time exposed individuals spend
actively moving over the sediment (horizontal activity). The
results of these experiments will form the basis of a prey
vulnerability submodel that will be integrated with the main
attack model in Section IV.

METHODS AND MATERIALS

Field Studies

The vertical activity of Crangonyx and Hyalella was observed
in both the laboratory and the field. In the field studies,

cores of sediment were removed from Marion Lake with a sampler, described by Hargrave (1970), and were transferred with as little disturbance as possible into glass stacking dishes (20 cm diameter). The natural complement of bottom fauna was not altered with the exception that in some dishes, the number of _Crangonyx_ was increased 2 to 5 times above the natural density. The dishes were then placed back into the lake to maintain them under ambient temperature and illumination.

After being transferred, the animals were allowed 24 hours to acclimate before observations were initiated. Each experimental series consisted of 4 replicate cores of sediment. During the study period both the incident radiation (Belfort, recording pyroheliograph) and the water temperature were monitored.

The vertical activity of _Crangonyx_ and _Hyalella_ was examined with respect to the average proportion of each population that was exposed above the mud-water interface during 15 consecutive, 10 second observation periods. Observations were conducted several times throughout the day (0800 to 1700 hrs.P.S.T.) and were repeated for for up to 4 consecutive days.

Eleven completely independent sets of experiments were conducted during the months of May, June and July. After the termination of each of these series the number of amphipods in each core was determined by sorting through the sediment. Preliminary trials indicated that this method would produce complete recovery.

Laboratory Studies

In the laboratory, the vertical as well as the activity
of exposed amphipods was observed at 4 different temperatures
that ranged from 5 to 20 C. For each experiment, amphipods
were removed from Marion Lake, sorted, and then isolated by
species into separate containers of sediment. In this case
the sediment had been screened to remove all other macroinver-
tebrates.

Three replicate populations of each species were observed
at each experimental temperature. Before observations were
conducted, the animals were allowed 24 hours to acclimate to
the experimental conditions. The number of animals in each
container was carefully controlled (equivalent to 100 to 300
Crangonyx, or 200 to 800 Hyalella per. sq. m.) to insure that
it fell within the natural range in density of each species
(Appendix III).

Throughout the experiments, the background illumination
was maintained at about 10 ft-candles, and the length of day
standardized at 10 hours (0900 to 1800 hrs P.S.T.). The water
temperature was controlled to within 1 C. of the desired test
temperature. In order to avoid the possibility of oxygen
depletion or stratification the water in each container was
slowly circulated.

Hyalella is a deposit feeding species (Hargrave , 1970)
and was not fed (artificially); Crangonyx, however, is carnivorous
and was fed dead brine shrimp. In this case, the amount of food

provided was always in excess of what the populations would consume between successive feedings. The mortality of both species during the experiments was less than 5%.

Observations on the vertical activity of Crangonyx and Hyalella were conducted before Crangonyx was fed and were repeated every 5 minutes for up to one hour. Their horizontal activity was expressed in terms of the average proportion of time exposed individuals spent moving over the sediment. In this case, observations were conducted at irregular intervals throughout the day.

RESULTS

THE EFFECT OF WATER TEMPERATURE ON THE VERTICAL ACTIVITY OF CRANGONYX AND HYALELLA

Under both natural and laboratory conditions, Crangonyx and Hyalella spend much of the day buried below the mud-water interface. When individuals are concealed in this fashion they tend to remain inactive for some time before they re-expose themselves; this characteristic behaviour was pointed out earlier (Section I). Intensive observations indicated that the instantaneous proportion of animals that was exposed was fairly constant over a short period of time but changed appreciably with the ambient environmental conditions.

A multiple regression analysis of the field studies showed that the vertical activity of amphipods was significantly correlated with several environmental parameters (Table 1). One of the most significant factors was water temperature. Although there is a strong correlation between the level of

incident radiation and the time of day observations were conducted, the ambient water temperature was not significantly affected by diel changes in the level of illumination.

Since the temperature of Marion Lake changes considerably throughout the year this characteristic of the environment could induce seasonal changes in the activity patterns of the amphipods. Therefore, the apparent relationship between water temperature and the degree of exposure of both populations was tested under controlled conditions.

Laboratory studies verified the field observation that the instantaneous proportion of animals that was exposed was temperature dependent. If the field data is grouped according to the temperature when observations were conducted both the laboratory and field results turn out to be very similar (figs. 1 and 2). This is interesting as the laboratory studies were extremely artificial compared to the field experiments.

It was found that the observed relationship between temperature and the proportion of amphipods at the mud-water interface could be described by the exponential equation:

$$(1) \quad VP_i = e^{M3_i (T) - M4_i}$$

where (VP_i) is the proportion of species (i) exposed at any instant in time, $(M3_i)$ and $(M4_i)$ are constants and (T) is the temperature in C. (fig. 1 and 2; Table 2A).

Although there was some indication that the illumination and time of day might have influenced the vertical movements

TABLE 1. The vertical dispersal activity of <u>Crangonyx</u> and <u>Hyalella</u>, in Marion Lake, with respect to several environmental conditions. (n) indicates the number of days in which observations were conducted.

Variable	Correlation Coefficient	t
	<u>Crangonyx</u>	
Illumination	0.229	1.56
Temperature	0.511	5.10 *
Time of day	- 0.102	0.70
	(n = 46)	
	<u>Hyalella</u>	
Illumination	0.576	4.65 *
Temperature	0.372	3.09*
Time of day	- 0.384	3.09 *
	(n = 43)	

* significant at or less than 0.01 level

Figure 1. The effect of water temperature on the

proportion of _Crangonyx_ that are exposed at or

above the mud-water interface. The solid circles

indicate the results obtained from laboratory

experiments; the open triangles, field experiments.

The 95% confidence intervals of each of the means

are indicated. (See Table 2A)

Crangonyx
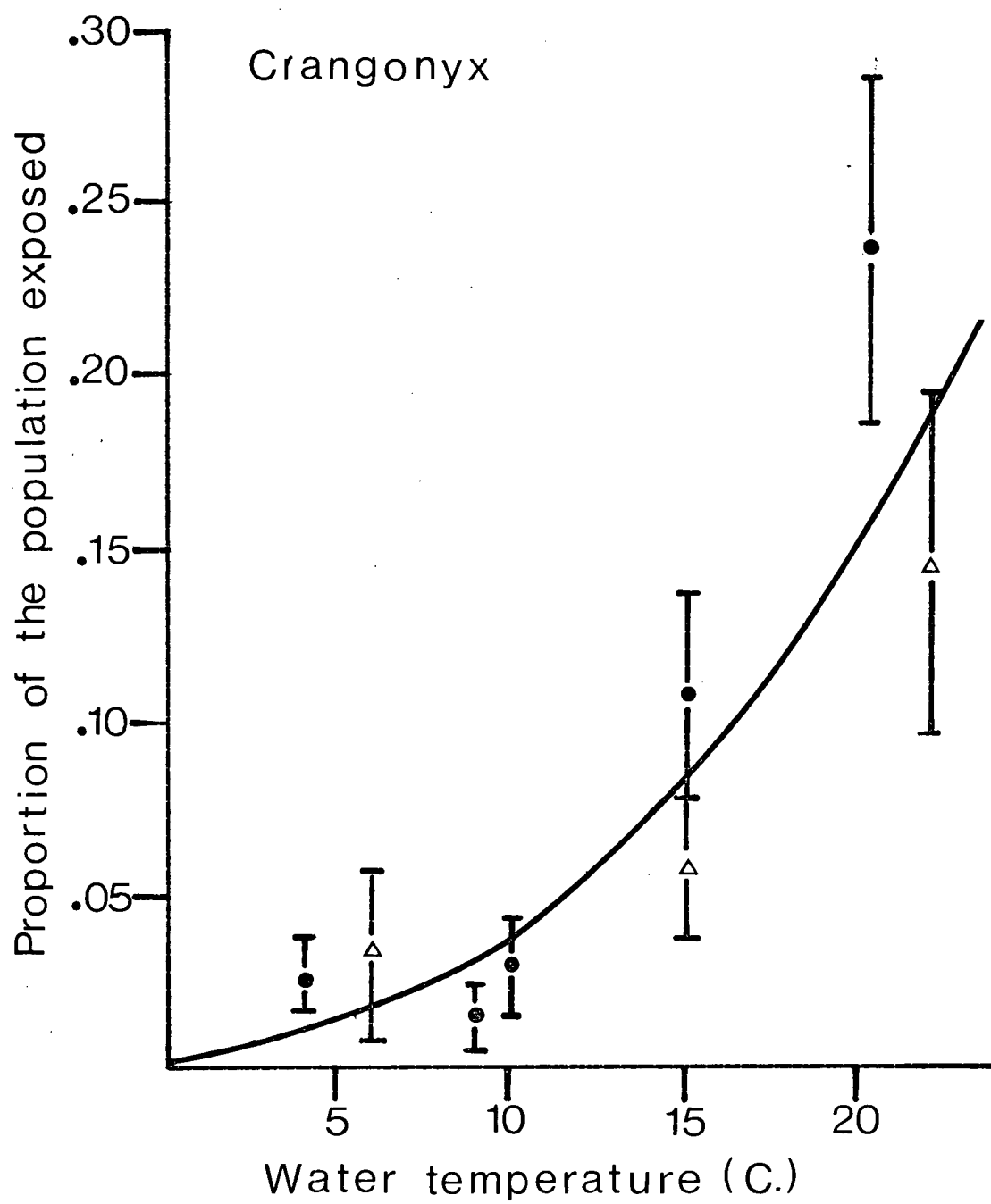
Figure 2. The effect of water temperature on the

proportion of _Hyalella_ that are exposed at or

above the mud-water interface. The solid circles

indicate the results obtained in the laboratory

experiments; the open triangles, field experiments.

The 95% confidence intervals of each of the means

are indicated. (See Table 2A)
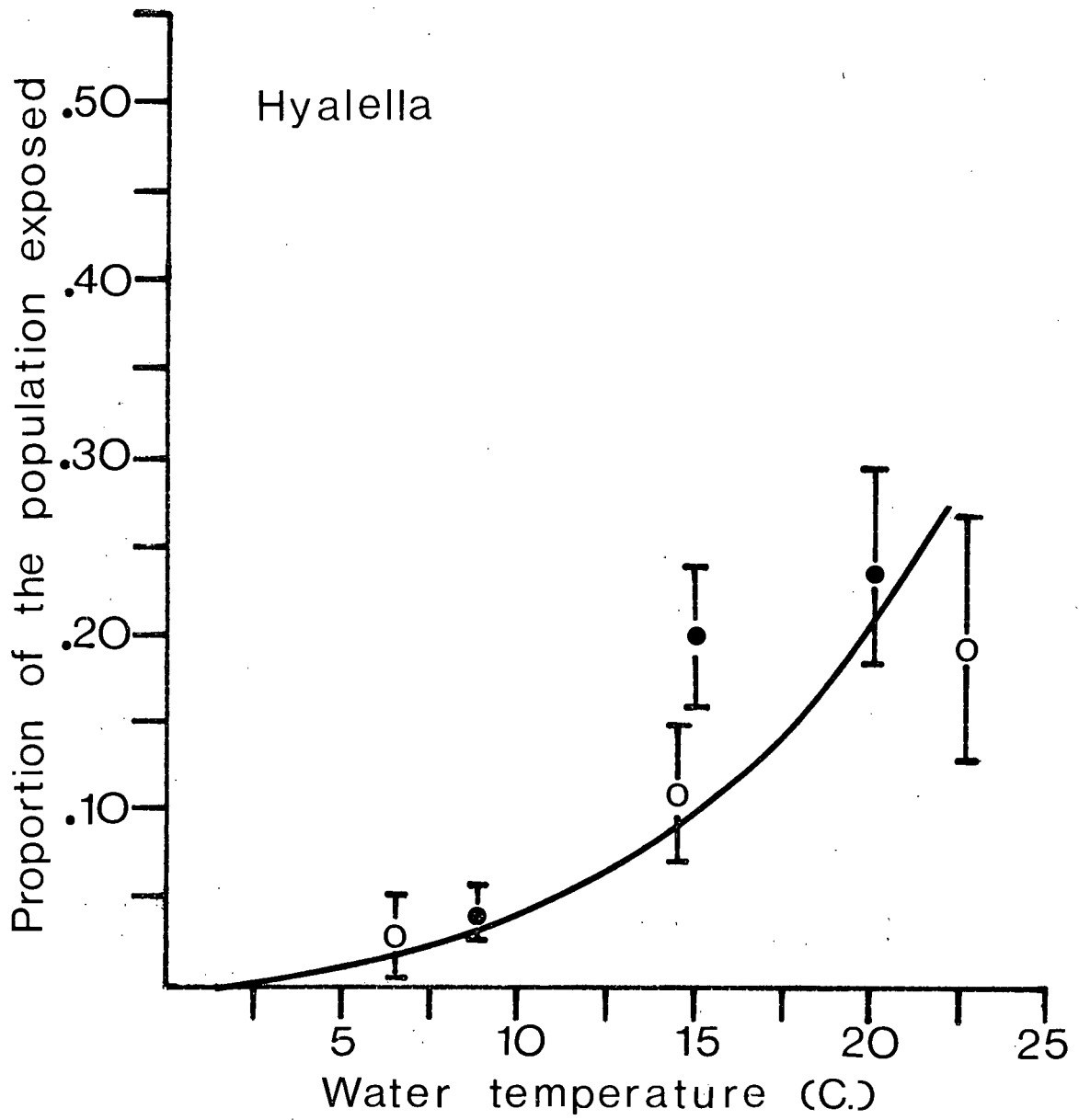
of _Crangonyx_ and especially _Hyalella_ (Table 1), none of these possibilities were followed up.

An expression of the density of amphipods, by size, per sq. m. that are potentially vulnerable to trout predation in Marion Lake at different times of the year can be derived by coupling equation (1) with the actual density of prey (D_i, Appendix III), the size composition of each population (P_{ij}) and the seasonal temperature pattern (Appendix II). The result is equation (2) which can be designated as a prey vulnerability submodel.

$$(2) \quad VN_{ij} = D_i \, P_{ij} \left[e^{M3_i (T)} - M4_i \right]$$

where (VN_{ij}) is the number of amphipods of species (i), of size (j) that are exposed. The seasonal range in the size structure of _Crangonyx_ and _Hyalella_ is summarized in Appendix III.

The profound effect that water temperature has on the vertical activity of the amphipods in Marion Lake is illustrated in Figure 3. As indicated, there is very little relationship between the actual density of either species and the number of animals that are exposed and vulnerable to attack from trout throughout the year. The vulnerable segment of each population was estimated from equation (2).

Figure 3. The relationship between the actual density of
    amphipods (white histograms) and their vulnerable density
    (black histograms). The vulnerable segment of each
    population corresponds to the number of animals that are
    exposed on the sediment as a result of the ambient water
    temperature (Appendix II) (A) Hyalella (B) Crangonyx

No. amphipods per sq. m.(X 100)

20   15   10   5

A

J F M A M J J A S O N D

Month

4   3   2   1

B

J F M A M J J A S O N D
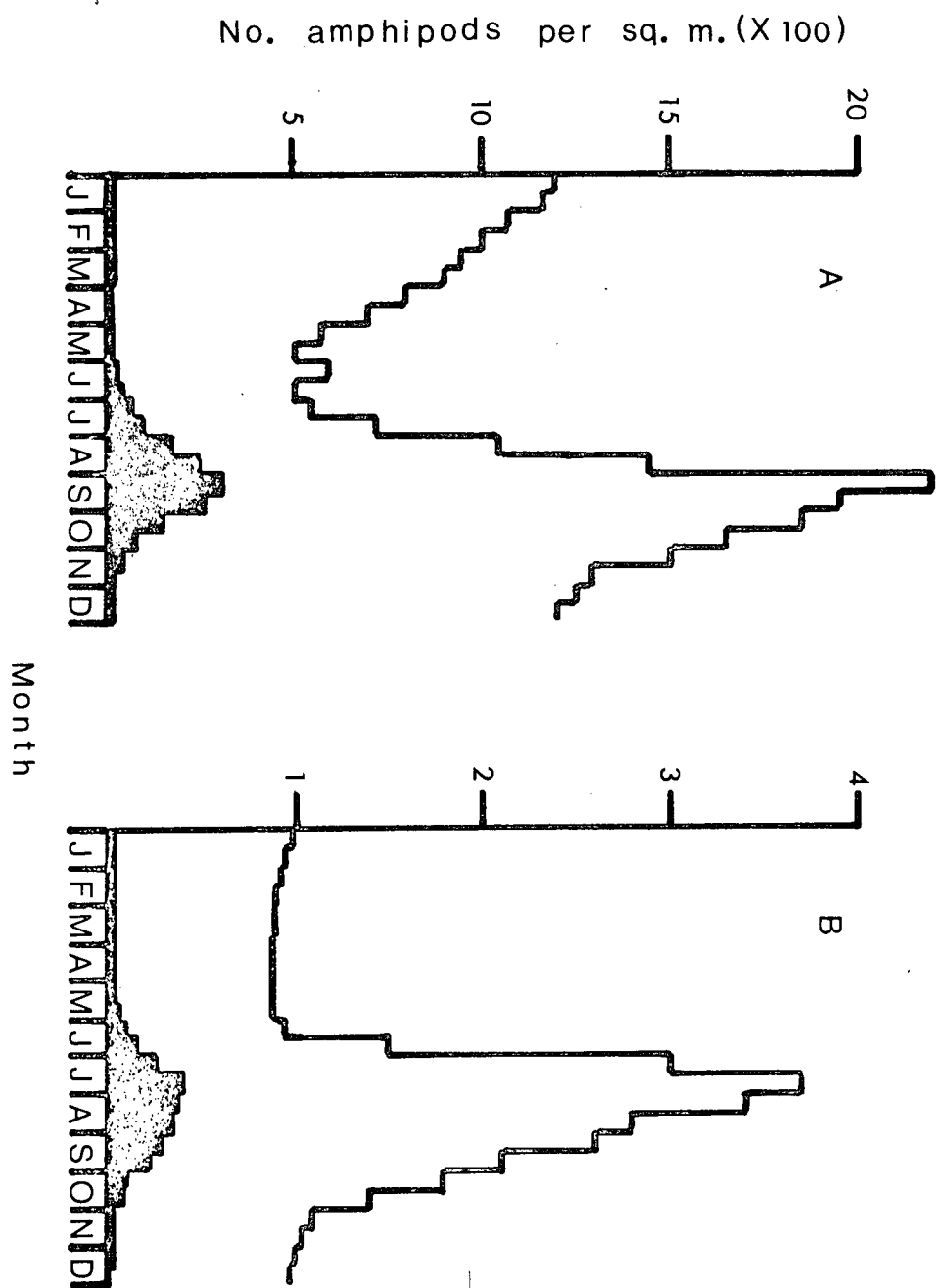
THE EFFECT OF TEMPERATURE ON THE ACTIVITY OF EXPOSED AMPHIPODS

Crangonyx tend to move almost continuously when exposed. They do stop periodically, however, to feed or to grasp at pieces of litter. In contrast, Hyalella tend to be relatively inactive at all times. Hargrave (1970) demonstrated that Hyalella is a deposit feeding species and must ingest large quantities of sediment to meet its energetic requirements. Thus, when this species is exposed it appears to spend most of its time either feeding or involved in other activities which seem to require little movement.

In the laboratory, the activity of exposed individuals was also affected by temperature. The results (fig. 4) suggest that 10°C. is the optimum for Crangonyx, above or below this, their activity declined somewhat. Unfortunately, observations on Hyalella were confined to temperatures above 10 C. At temperatures higher than this, their activity also declined which suggests that they may have an optimum temperature which is similar to Crangonyx. Although the water temperature will alter the movement of both species, Crangonyx was always more active than Hyalella.

Assuming that amphipods are most active at 10°C. the effect of water temperature on their general level of activity can be described by the parabola:

$$(3) \quad PA_i = M5_i + M6_i (T) - M7_i (T^2)$$

in which case, PA_i is the proportion of time an individual of species (i) will spend moving when exposed; $M5_i$, $M6_i$, and $M7_i$ are constants that can be estimated by fitting the data in Figure 4 by multiple regression (Table 2B).

The results presented above demonstrate that the ambient water temperature will alter the proportion of animals that are vulnerable to attack from trout as well as the activity of exposed amphipods. It was necessary to consider the effect of temperature on the movements of vulnerable animals because trout will react to moving prey from a considerably greater distance than stationary objects of the same size. The significance of this observation will become apparent in the next section.

Figure 4. The relationship between water temperature
and the average amount of time exposed Crangonyx
(A) and Hyalella (B) spend moving. The optimum
temperature for the activity of both species is
assumed to be 10 C. (See Table 2B)
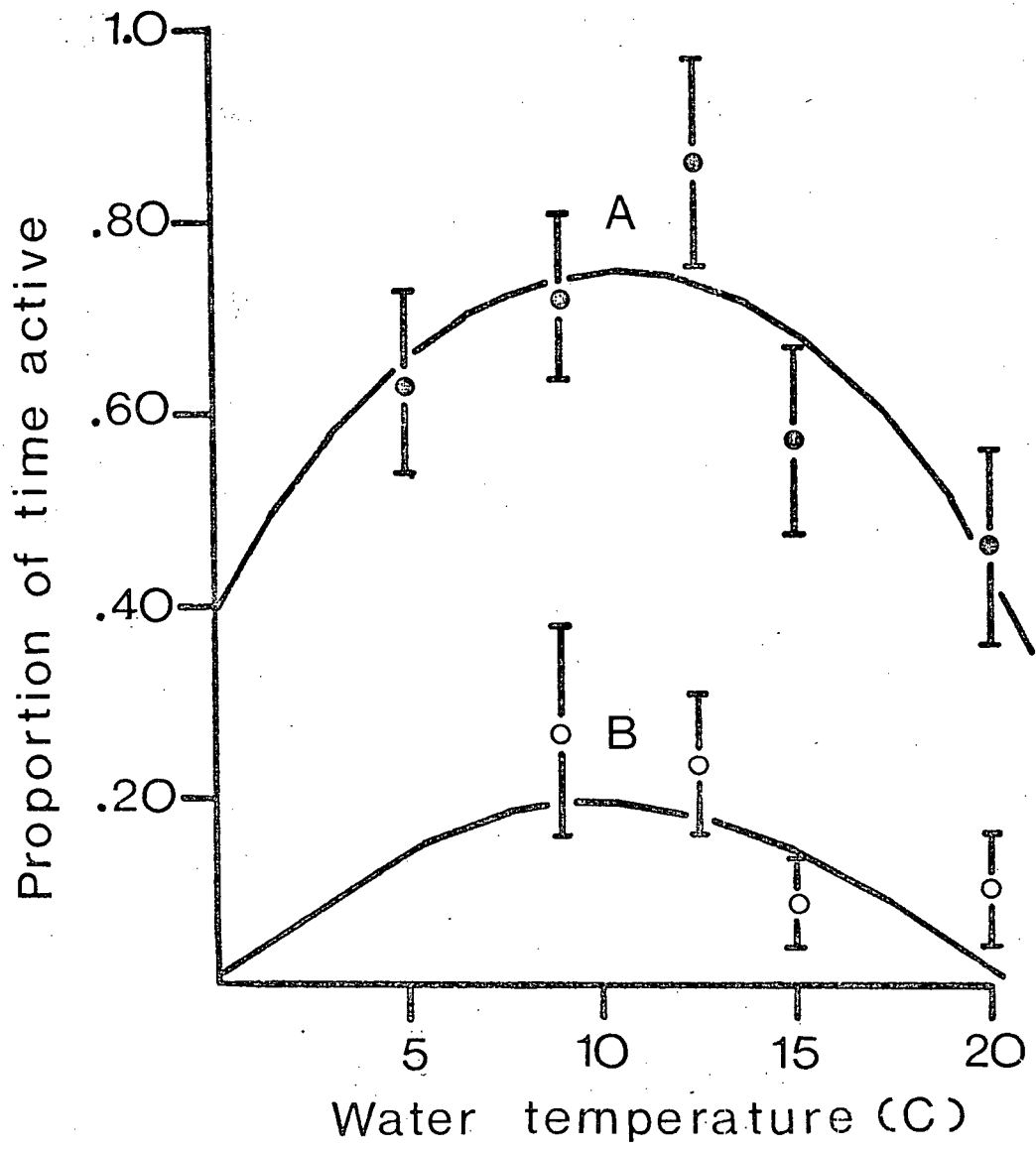
TABLE 2

A.

The relationship between the ambient water temperature (T) and the instantaneous proportion of <u>Crangonyx</u> and <u>Hyalella</u> exposed at or above the mud-water interface (VP_i). (R^2) is the amount of variability accounted for by the regression and (P) is the probability that the slope is zero (no correlation).

Species ($_i$)	M3($_i$)	M4($_i$)	R^2	P
<u>Crangonyx</u>	0.138	4.63	0.81	0.0027
<u>Hyalella</u>	0.180	5.13	0.84	0.010

B.

The relationship between the ambient water temperature (T) and the average proportion of time exposed, amphipods spend moving. (R^2) is the amount of variability accounted for by the regression.

Species ($_i$)	M5($_i$)	M6($_i$) $\pm$ 1 SE		M7($_i$) $\pm$ 1SE		R^2
<u>Crangonyx</u>	0.39	0.069	0.069	0.0033	0.0027	0.58
<u>Hyalella</u>	0.01	0.039	0.049	0.0017	0.0019	0.34

SECTION IV

A SIMULATION MODEL OF THE PREDATORY BEHAVIOUR OF TROUT

INTRODUCTION

One of the most common observations of trophic ecology is that many animals do not exploit prey in direct proportion to their abundance and, therefore, feed selectively (Lindstrom, 1955; Ivlev , 1961). Ivlev was well aware of this phenomenon and devised the term 'electivity' to describe how animals exploit different food organisms. Although 'electivity' indices or similar expressions are useful as descriptive statements, they provide no insight into, or explanation of, the mechanisms responsible for 'selective' predation. Until these mechanisms are identified, there is little hope of arriving at a set of generalizations to account for this phenomenon, which, as Ivlev (1961) pointed out, has tremendous significance both to evolutionary biologists (i.e. Batesian mimicry) and community ecologists (i.e. energy transfer).

There is sufficient evidence in the literature to suggest that the action of any one of three basic components of the feeding process: 1) prey detection, 2) prey handling, and 3) learning behaviour, could result in 'selective' predation. These components operate at different stages in the feeding process and some, such as learning, may not be common to all animals. Prey detection, however, is a fundamental stage in the feeding of all animals, except, perhaps, filter feeders.

Every sensory system is limited in its capacity to receive information and depending upon its mode of operation is biased toward detecting certain types of signals ('adequate stimulus'). For example, the process of visual discrimination is highly sensitive to both the size and contrast of a target (le Grand, 1967; Hester, 1968); while chemoreceptors are sensitive to the concentration and nature of the stimulus. Predators will 'selectively' detect some species if they react differently to the stimuli emitted by prey. If food selection can be explained simply on the basis of the process of discrimination it can be referred to as perceptual selection.

Most predators cannot successfully pursue (Ivlev, 1961) or capture (Dixon, 1959; Holling, 1964) every prey they detect. At some point, the ability of an animal to capture food is likely to be dependent upon prey size. In the animals in which this has been looked at there tends to be an optimum sized prey that can be handled most successfully. Therefore selection can also operate at this level. If food selection can be explained on the basis of differential capture success it can be referred to as mechanical selection.

Finally, many animals have the capacity to learn and thereby alter their response to prey through experience (Croze, 1970; Beukema, 1968). In the learning process the palatability of a food is of major importance. Most animals will learn to avoid unpalatable objects (Holling, 1965; Morrell and Turner, 1970; Prop, 1960) but will increase their responsiveness to more palatable prey (Section II; Beukema, 1968). Therefore, learning

could also be responsible for the disproportionate exploitation of some prey by predators. Selection at this level can be referred to as behavioural selection.

In this section I will examine the process of prey detection and recognition, and test the hypothesis that the selective exploitation of several invertebrate prey (especially the amphipods) by the trout population in Marion Lake can be explained at the perceptual level. Since the simulation model that will be developed to test this hypothesis will not consider the effects of hunger or learning, among other things, it is not intended to be a complete description of the predatory behaviour of trout. The model however, was structured so that it could be easily modified to incorporate these components as more information became available.

METHODS AND MATERIALS

Nine rainbow trout which ranged in length from 11 to 14 cm. were obtained from Marion Lake. After the fish were transferred to the laboratory a month of preliminary experiments were conducted to habituate them to being handled and to condition them to respond to artificial food.

The test prey were formed from pieces of chicken liver. Preliminary experiments indicated that the fish considered this food to be palatable as they would avidly consume it; they would not respond to other 'less palatable' foods this readily. Throughout the experiments, the form of the prey was standardized (rectangular)

The characteristics of target size, contrast and motion were altered, however, to determine how trout would react to prey with different visual properties. The size of the prey was altered simply by changing their length and holding their width constant (3 n.m).

The inherent contrast of a target (C_0) can be defined as the difference in luminous flux reflected by the object (L') with respect to the background (R) (le Grand, 1967). That is,

$$C_0 = \frac{R - L'}{R}$$

Two levels of contrast were examined. In one case, pieces of liver were stained 'black' by immersing them in a saturated solution of Sudan Black B (water insoluble stain). For the other level of contrast the prey retained the natural color of liver ('white'). The inherent contrast of both the 'white' and 'black' prey was determined with a photometer (Photovolt, model 200) with a neutral density filter. Under the experimental conditions the background (tank bottom) reflected 0.3 ft.-candles, the inherent contrast of the undyed prey was found to be 0.67 and that of the 'black' prey, 0.14.

Once the fish had been conditioned to respond to artificial food, the distance from which they would react was observed in a large rectangular tank (180 x 16 x 30 cm), constructed of clear plexiglass. At one end, there was a small holding chamber with an opaque, sliding partition that was used to isolate the fish

before an experiment. While the fish was in the holding area
a prey of known size and contrast was placed into the tank.
The trout was then released and the distance from which it
would react was recorded. After an attack was completed the
predator was returned to the holding area while another prey
was introduced. The position of the food was randomized between
successive trials. Up to 10 successive attacks were recorded
for each fish during a test period.

The hunger level of the fish was standardized by adopting
a 48 to 72 hour period of food deprivation between successive
experiments. This was known to be sufficient time to completely
clear all the food consumed during the previous meal from the
digestive tract. An additional series of tests demonstrated
that the reactive distance was not affected by short term
changes in hunger. If the predators were fed up to 50% of
the maximum amount of food they could ingest, they reacted from
the same distance as they would after a 48 to 72 hour period
of food deprivation. Therefore the slight change in hunger
that occurred during an experiment was unlikely to have affected
the distance from which the trout attacked.

The effect of prey motion on reactive distance was examined
by placing standard 'white' or 'black' targets on a small platform
that moved vertically to simulate a slow moving animal (3 mm
per sec.). Control tests demonstrated that the fish would
respond only if the platform was supporting food.

The experiments dealing with the effect of background diversity
on reactive distance and prey recognition success were conducted

under the same conditions as those described above. Except in this case, the background was altered ('broken') to simulate a diverse substrate. The element of diversity was created by scattering small, 'black' pebbles, the same size and contrast as the prey (5 mm; contrast = 0.14), uniformly over the bottom of the tank. The mean distance between adjacent pebbles was in the order of 0.5 cm.

Before a predator was released, a single prey was placed at random into the tank. The distance from the trout attacked both stationary and moving targets as well as their ability to recognize prey under these conditions was recorded. A failure in recognition was considered to have occurred if a fish passed by a potential target without attacking. Recognition success, therefore, was defined as the ratio of the number of attacks that were initiated to the number of opportunities the fish had to discover prey. These experiments were replicated over 6 days to determine if the performance of the trout would improve with experience.

RESULTS

THE CHARACTERISTICS OF THE VISUAL RESPONSE OF RAINBOW TROUT TO PREY

The Relationship Between Prey Size and Contrast Threshold

Since the aim of this section is to develop a model to describe the response of a visual predator, such as rainbow trout, to prey it would be desirable to seek generality and, therefore, interpret the process of prey detection in terms

of a general theory of visual discrimination.

The inherent contrast of an object was defined as the amount of light it reflects with respect to the background when the distance between it and an observer is zero. Due to scattering and absorption of reflected light by the bakcground, this contrast will appear to diminish as one moves further away from the object. Duntley (1963) and le Grand (1967) as well as others have found that the relationship between distance and apparent contrast can be described by the negative exponential equation:

$$(1) \quad C_a = C_o e^{- 6 (X)}$$

where C_a = the apparent contrast of a target at distance
                   (X),

         C_o = the inherent contrast of a target (X = 0),

         6   =   the rate of extinction of target contrast.

The attenuation coefficient (6) should be specified in terms of the wavelengths of reflected light because longer wavelengths are absorbed most rapidly in water (Sverdrup et al, 1942). However, the addition of this component would add considerable complexity to the model, therefore, (6) was defined simply in terms of the total attenuation of light irrespective of wavelength.

The rate of attenuation was determined by measuring the inherent contrast of the prey (photometer with a neutral density filter) under the standard experimental conditions as

well as their apparent contrast at a distance of 1 meter.
Equation (1) was then solved to estimate (6). The value
of this parameter was found to be about 0.50 for both dyed
and unstained targets.

In the study of visual discrimination it is conventional
to express the size of a target in terms of the visual angle
it subtends with the retina of an observer. This angle (S)
is defined as:

$$(2) \quad S = \tan \theta = TD/X$$

where (TD) is the length of diameter of a target and (X) is
the distance between it and an observer.

In the present study the relationship between the visual
angle prey subtended with trout and the apparent contrast they
presented when they were attacked can be described if the
reactive distance is expressed as a visual angle. The average
distance 4 trout reacted to different sizes of prey (inherent
contrast, 0.14) is indicated in Table 1. These data were
transformed to a visual angle by substituting (RD) for (X) in
equation (2) and solving for (S). It was also possible to
estimate the apparent contrast of each target, when the fish
attacked, because the inherent contrast of the prey (C_o) and
the attenuation rate (6) were known.

The apparent contrast was calculated by substituting the
reactive distance (RD) for (X) in equation (1) and solving for
(Ca). The results of this transformation (CT) are presented

TABLE 1. The relationship between prey size (TD) and the average reactive distance (RD). (CT) is the apparent contrast of the black prey* and (S) is the visual angle they subtended when they were attacked. The results were obtained from replicate experiments with 4 fish, (n) indicates the total number of observations.

TD (m)	n	RD (m) $\pm$ 1 S.E.		CT	S (min)
.0020	20	.20	.017	.127	34
.0035	20	.30	.017	.120	40
.005	20	.32	.018	.119	54
.006	20	.37	.019	.116	56
.009	20	.44	.022	.112	70
.012	20	.49	.018	.109	84
.015	20	.52	.018	.108	100

* inherent contrast ($C_0 = 0.14$)

in Table 1.

Although the trout responded to large prey from a greater distance than smaller targets the relationship was not linear (Table 1). Another way of stating this observation is that there was an inverse relation between the visual angle that a prey subtended and its apparent contrast (CT) when it was attacked. This is diagramatically illustrated in Figure 1. There are two limits to this function, however, that are not apparent from the experimental data (Table 1). The first characteristic is that there is a minimum level of contrast (CT_{min}) that can just be discriminated by a visual animal. If the apparent contrast of a target does not exceed this level then it cannot be detected (fig. 1). Secondly, there is also a minimum visual angle (S_{min}) that must be subtended before a target can be discriminated. The performance of any visual system is restricted by these two limits of resolution (Hester, 1968; le Grand, 1967).

If these appropriate limits are defined, the relationship depicted in Figure 1 can be described by the negative expotential equation:

$$(5) \quad CT = (CM)e^{L - B (\ln(S))}$$

In which case, (L) and (B) are constants and (CM) is the contrast threshold when a prey subtends the minimum visual angle (S_{min}). The restrictions of equation 3 were illustrated in figure 1 and can be summarized as follows:

Figure 1. A diagramatic representation of the relationship
between the contrast threshold, or the apparent contrast
a target must have in order to be discriminated, and the
visual angle it subtends with the eye of an observer. The
two limits to this function are (CT_{min}) and (S_{min}); (CT_{min})
is the minimum level of contrast that can be detected,
while (S_{min}) is the smallest, or minimum visual angle a
target can subtend and still be discriminated. The point
(CM) is the contrast threshold for a target which subtends
the minimum visual angle at a specified level of illumination.
Curve (A) simulates the function at a low level of illumination
curve (B), at a somewhat higher level.
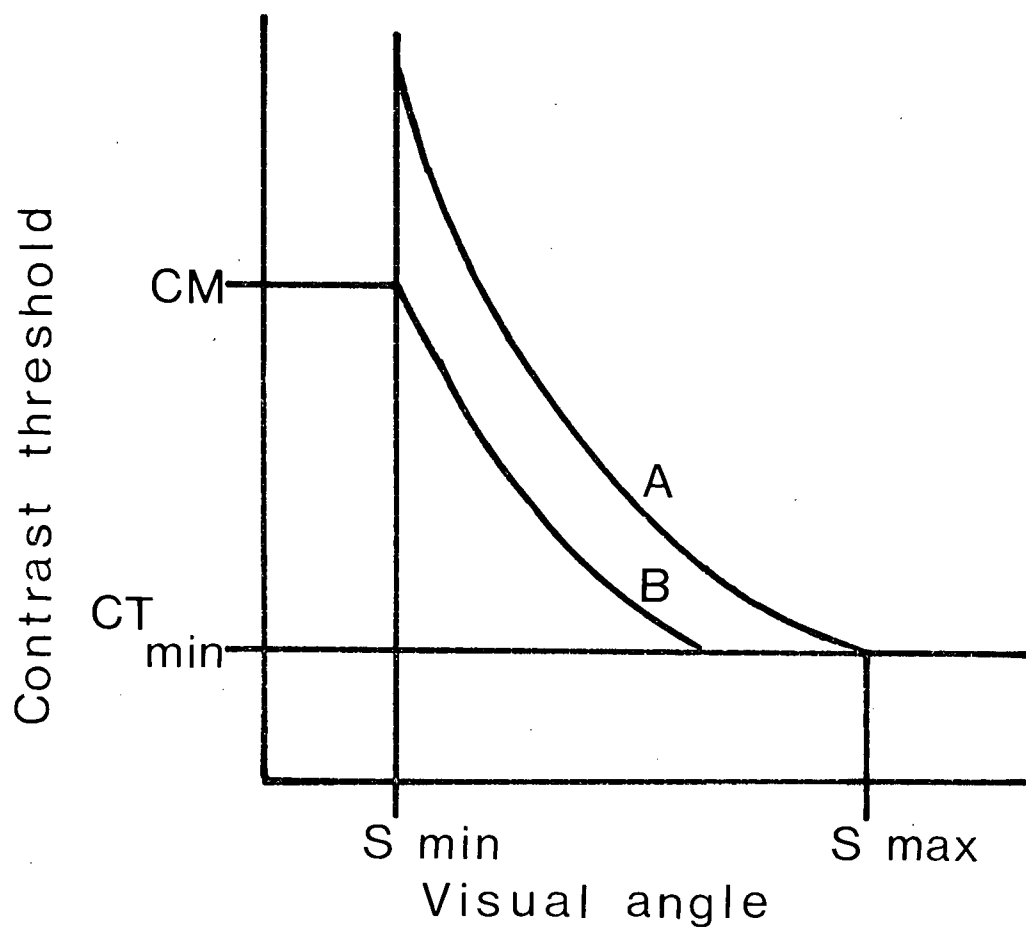
1) (S) cannot be less than (S_{min}),

2) (CT) cannot be less than (CT_{min}).

Some additional information is required, however, before the constants of equation (3) can be estimated. In the present study, neither the minimum visual angle nor the minimum contrast threshold of trout were obtained. Values for each of these parameters, however, have been reported for other animals (Table 2). Therefore I have assumed that 0.05 is the minimum contrast that trout can discriminate (after Hester, 1968) and that their minimum visual angle is in the order of 5 minutes of arc (Nakamura, 1968; Yamanouchi, 1956; Tamura, 1957). Although neither of these parameters were measured directly for trout, they represent values that have been found for fish that have well developed visual systems.

If the data in Table 1 are transformed to logarithms and $\ln (CT)$ is regressed against $\ln (S)$, the contrast threshold (CM) when a target subtends a visual angle of 5 minutes of arc can be estimated, for trout, by extrapolation. Once this value is obtained the remaining parameters of equation (3) can be derived by regressing $\ln (CM/CT)$ against $\ln(S)$. In which case, (B) is the slope of the line and (L) is the Y-intercept. A regression analysis demonstrated that the data in Table 1 could be adequately described by a straight line ($r = 0.94$); the estimated values of (B) and (L) are presented in Table 5.

The Relation Between the Ambient Illumination, Visual Angle and Contrast Threshold

It is well documented that the background illumination also affects the process of visual discrimination. This is illustrated in Figure 1, where curve (A) simulates the relationship between the visual angle and contrast threshold at a low level of illumination, and curve (B), the function at a somewhat higher level. Thus, for any angle less than (S_{max}) the contrast required for discrimination will decrease if the background illumination is raised. This means that a visual predator will be able to detect prey from a greater distance at higher levels of illumination. This relationship, however, only holds over a specified range. Before any optical system can function the ambient illumination must surpass some lower threshold (R_{min}). On the other hand, once the illumination reaches some upper level (R_{max}) the system will perform maximally. Any further increase in the background illumination will not improve this performance. Several reported estimates of the upper and lower levels of illumination that affect the visual acuity of fish are presented in Table 2.

The influence of illumination can be described through its effect on the component (CM). Hester (1968) and le Grand (1967) have shown that (CM) diminishes at a decreasing rate if the background illumination is raised from the limit of scotopic vision (R_{min}) to (R_{max}). This relationship can be approximated by the negative exponential equation:

TABLE 2. A comparison of several documented values of the minimum detectable contrast (CT_{min}) and the minimum visual angle (S_{min}) of different animals. (R_{min}) is the limit of scotopic vision and (R_{max}) is the lowest level of illumination which produces maximum visual acuity.

Animal	CT_{min}	S_{min} (a)	R_{max} (b)	R_{min} (b)	Source
Human	0.01	0.5	30	3.0×10^{-7}	le Grand, 1967
Goldfish	0.05	20.0	10	1.0×10^{-2}	Hester, 1968
Herring		25.0		1.0×10^{-4}	Blaxter, 1968 b
Salmon (6sp.)			1 - 10	1.0×10^{-4}	Ali, 1959
Plaice				1.0×10^{-4}	Blaxter, 1968 a
Marine Teleosts	4.0 - 15.0				Tamura, 1957
Skipjack Tuna		5.0	10	1.0×10^{-3}	Nakamura, 1968
Jack mackerel			12	1.0×10^{-7}	Hunter, 1968

a   angle expressed in minutes of arc.

b   the level of illumination in ft-candles

$$(4) \quad CM = K_1 \quad e^{-\ A(R)}$$

where (K_1) is the contrast a prey must have to be attacked when it subtends the minimum visual angle and the ambient illumination is at the predator's scotopic limit of vision (R_{min}); (A) is simply a rate constant and (R) is the level of illumination.

The value of (A) was calculated from Hester's (1968) data (Table 5). Although (K_1) was not specifically measured for trout, it can be estimated by substituting the value of (CM) (Table 5) at the standard level of illumination $(R = 0.03$ ft-candles) into (4).

Equation (4) can now be coupled with (3) to obtain a single expression which includes the effect of both the ambient illumination and prey size on the apparent contrast trout require to discriminate a target. The result is,

$$(5) \quad CT_. = K_1 \quad e^{-[A\ R]\ +\ [L\ -\ B\ (\ \ln\ (S))]}$$

The inclusion of ambient illumination, however, imposes two additional restraints on equation (5) other than those already mentioned in conjunction with (3):

3) a target cannot be detected if (R) is less than (R_{min}).

4) K_1 reaches a minimum value when $(R) = (R_{max})$.

Now that the relationship between the illumination, the visual angle and the contrast threshold has been described, it is necessary to convert this expression into the average

distance trout will react to different sizes of prey. This

transformation can be accomplished by iteratively solving

equations (1) and (5) until a distance (X) is found which

satisfies the equality (C_a = CT). In the model, a computer

program was designed to undertake this operation.

Figure 2 presents a comparison between the actual reactive

distance (Table 1) and the distance that was generated in each

case, by iteratively solving (1) and (5). The close agreement

between the observed and calculated distance of attack indicates

that the equations that have been developed do describe the

experimental results reasonably well and that little accuracy

has been lost by transforming the original data. The other

point illustrated in Figure 2 is that the distance of reaction

is tending towards a maximum. The upper limit to the attack

distance will occur when the apparent contrast of the target

is equal to the minimum level of contrast the animal can

discriminate (CT_{min}).

The Effect of Prey Movement on Reactive Distance

It has been shown that the distance from which trout

will attack depends upon several characteristics of a prey

as well as the environment. The equations that were developed

to describe these effects were based upon the reaction of trout

to stationary prey. Therefore an additional series of experiments

was conducted to determine if the predators would respond

differently to moving prey. The prey in this case had a high

Figure 2. A comparison between the observed reactive

distance (data points) of 4 trout, exposed to different

sizes of prey, and the calculated reactive distance

(curve). The latter was obtained by solving equations

(1) and (5). See text for further explanation. The

95% confidence limits of the means are indicated by the

vertical bars.
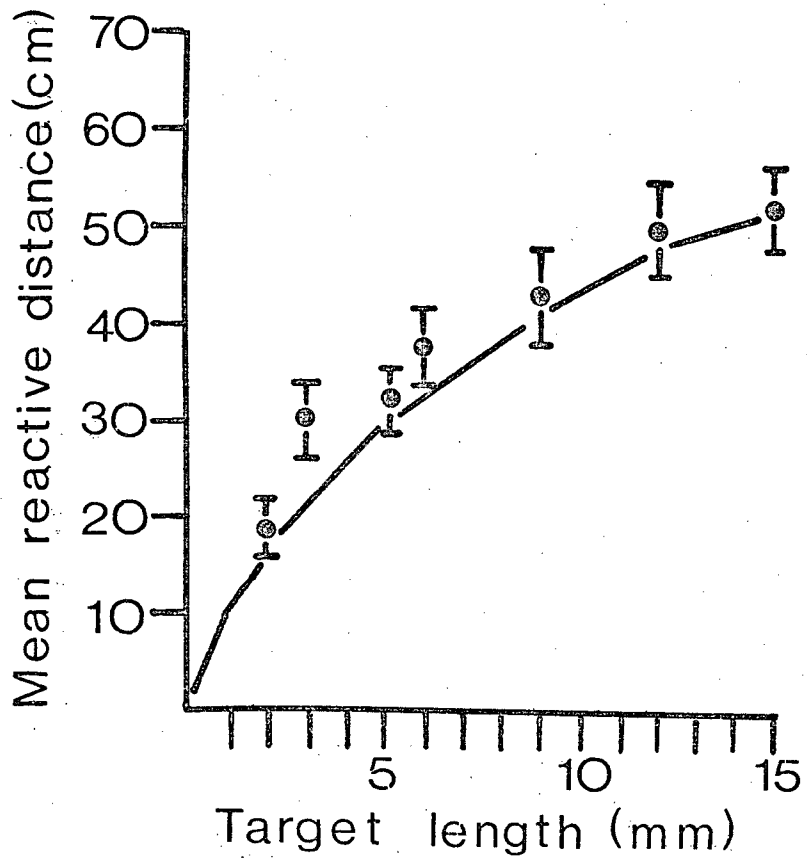
Figure 3.   The effect of target movement on reactive

distance.   The open circles indicate the average

reactive distance (4 fish) for stationary prey of

different sizes (inherent contrast = 0.67).   The

solid circles show the average reactive distance

for moving prey of the same size and contrast.   The

95% confidence limits of the means are indicated.
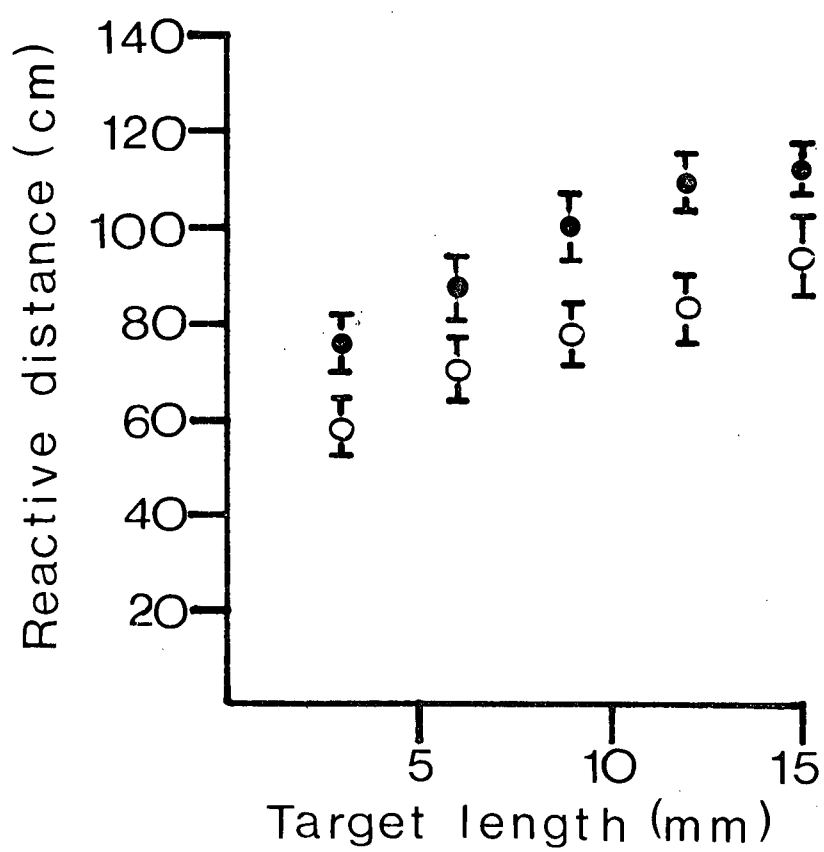
level of contrast (0.67).

In the first experiment, 4 trout were exposed to stationary prey of different sizes, and the average distance from which they would react was recorded. Once these trials were completed the fish were switched to moving prey with the same level of contrast. The results (fig. 3) clearly show that trout will attack moving prey from a significantly greater distance than stationary objects with the same visual properties. At least over the range in size that was investigated, the effect of target motion was additive because the trout would react to moving prey 22 cm further away than they would to stationary targets of the same size.

If the distance from which trout will attack a stationary object of a given size and contrast (j) is defined as (R_j), then the effect of motion on the distance of reaction can be expressed as:

$$(6) \quad R_j' = R_j + MC$$

where, (MC) is the increment effect of motion.

For the purposes of this paper, I will assume that the additive effect of motion is independent of the velocity of the target and the background illumination.

The Relation Between the Background, Reactive Distance and Prey Recognition Success

When a prey was the only object in the tank and was

contrasted against a flat, evenly illuminated surface ('smooth')
the trout were 100% successful in recognizing it regardless
of whether it was stationary or moving. However, if the background
was diversified ('broken') in the sense that other similar but
non-prey objects were scattered over the surface to break up
the uniformity, then the trout's ability to discriminate or
recognize prey might be somewhat impared. A 'broken' surface
might also alter the reactive distance. Both of these
possibilities are worth investigating because Crangonyx and
Hyalella, as well as other invertebrates in Marion Lake, are
exceedingly cryptic and live in association with a very diverse
background, the sediment.

Table 3 presents the results of some experiments which
demonstrate that the presence of other objects can diminish
the success trout have in discriminating prey. Under these
conditions, the fish were less than 100% successful in discovering
both stationary and moving targets, although they were considerably
more successful in recognizing moving prey. The effect of the
background on recognition success will be incorporated into the
model at a later stage.

In these experiments, a reduction in recognition success
was not the only change that occurred, the reactive distance
was also diminished by a factor of about 4 (Table 4). Apparently,
when the background is 'broken' trout require a higher level of
apparent contrast before they will attack. If (E) is defined
as a proportionality constant which describes the distance

TABLE 3. The effect of background diversity on the probability that trout will successfully recognize a 5 mm prey (inherent contrast = 0.14). (n) indicates the number of replicate experiments (4 fish). The 95% confidence intervals of the means are presented.

Target	n	$\overline{X}$ Probability of recognition
Stationary	8	0.39 ± 0.12
Moving	8	0.74 ± 0.25

TABLE 4. The effect of the background on reactive distance.
In each case, the prey were 5 mm and had an inherent contrast
of 0.14. (n) indicates the number of observations obtained
from 4 trout; (E) is the proportional difference in the reactive
distance in a 'broken' environment with respect to the distance
in a 'smooth' environment.

Target	Background	n	Mean Reactive Distance * (cm)
Stationary	'smooth'	44	35.0 ± 2.0
Stationary	'broken'	52	8.0 ± 1.9
			E = 0.23

* the 95% confidence intervals of the means are indicated.

from which trout will react in a 'broken' environment with respect to their response when prey are contrasted against a 'smooth' background, then equation (6) can be modified to express the distance of reaction in a 'broken' environment (RD_j) as follows:

$$(7) \quad RD_j = (R_j)E, \quad \text{for stationary prey and,}$$

$$(8) \quad RD_j' = (R_j')E, \quad \text{if the prey is moving.}$$

The relationship between the background and reactive distance has been treated very superficially. Ideally, one should determine if the effect of the background is independent of prey size, as well as investigate the functional relationship between different degrees of complexity and the distance of reaction. For this study, however, the estimated value of (E) is considered to approximate the conditions in Marion Lake. The experimental background attempted to simulate the diversity of the sediment.

The Effect of Prey Activity and the Searching Position on the Width of the Path of Search

Trout, like most teleosts, have a field of vision that almost encompasses a full 360 degrees. In most fishes, however, the density of cones in the retina is not completely uniform

therefore the visual field is not in fact completely spherical
(Tamura, 1957; Hester, 1968). Nevertheless, I will assume
that the visual field can be described as a solid sphere. Since
it has been shown that the reactive distance is dependent upon
the visual characteristics of a prey, the dimensions of the
reactive field must be qualified. In other words, for every
prey (j) there is a spherical field about a predator in which
it is responsive to this object. The radius of this field is
defined as the reactive distance or (RD_j). At the moment I
am only considering stationary prey.

Rainbow trout characteristically adopt a searching position
some 10 to 15 cm above the sediment when they hunt for benthic
food organisms. Although this may not appear to be very significant
I suggested in another study (Section I) that this behaviour
might in fact create a refuge for some prey. For if the height
of the predator's searching position ever exceeds the distance
it requires to discriminate prey then those animals will be
invulnerable to attack. This inference,however, is only the
limiting condition of a more general phenomenon. That is, as
a predator moves further away from the sediment the width of
the path it sweeps along the bottom will diminish and approach
zero (fig. 4). Once this occurs prey (j) will be invulnerable
to attack.

Since we are only interested in the amount of sediment a
trout will effectively search when it is hunting for bottom
living animals, the width of this path (EP_j) will be determined

Figure 4. The geometric relationship between the radius

    of the reactive field (RDj), the trout's searching

    position (SP) and the effective width of their searching

    path along the sediment (EPj). The position of the fish

    is simulated by the solid circle in the center of the

    reactive field. In order to be attacked, a prey (j)

    must be within the path of search.

SP

RDi

FRj-1

EPj

RDj

FRj

EPj
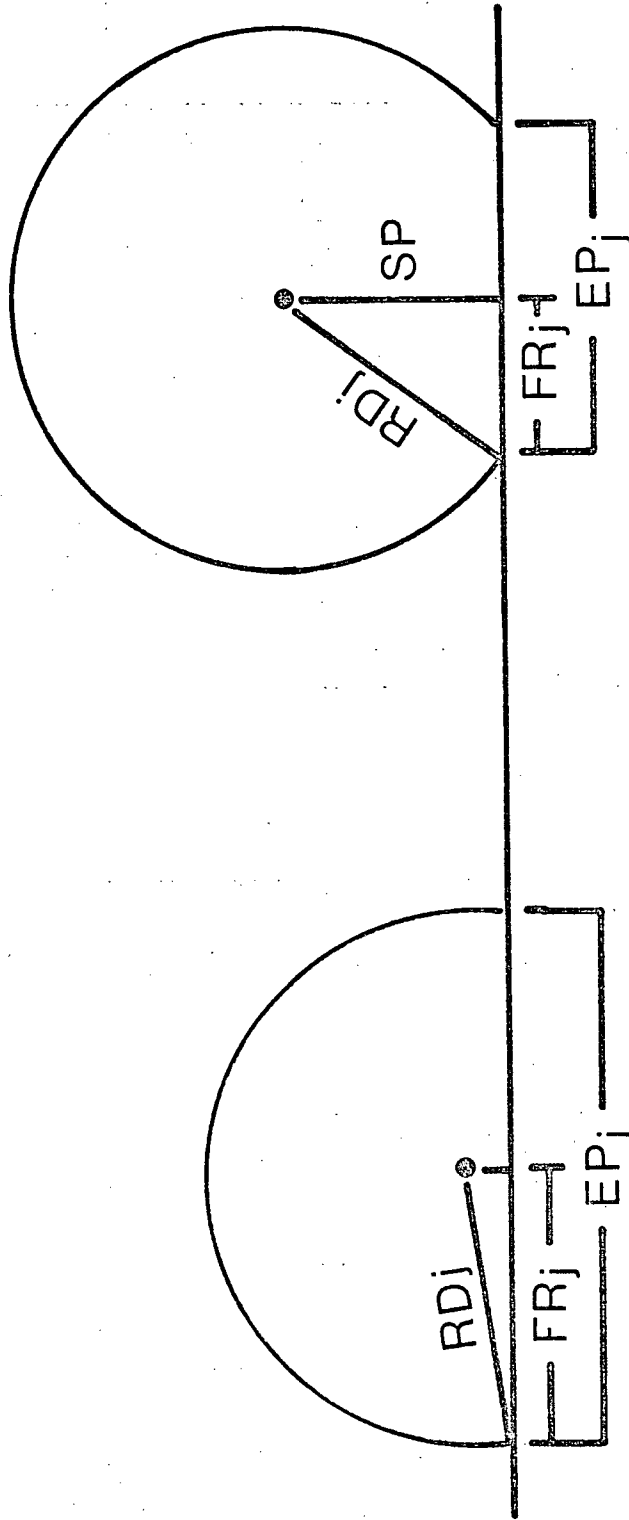
by the simple geometric relationship between the radius of the
reactive field (RD_j) and the height of the predator's searching
position (SP) (fig. 4). That is,

$$(9) \quad FR_j = (RD_j^2 - SP^2)^{\frac{1}{2}}$$

since $\quad\quad EP_j = 2 FR_j$

then, $\quad (10) \; EP_j = 2 (RD_j^2 - SP^2)^{\frac{1}{2}}$

The effect of prey motion can be incorporated into the
model at this point in a rather simple way by weighting the
radius of the reactive field according to the proportion of
prey that are active (PA_i). In other words, if (RD_j) and
(RD_j') are respectively, the radii of the reactive field for
moving and stationary prey, then the average radius of the
reactive field for a prey (j) of species (i) is given by:

$$\overline{RD}_{ij} = \Big[(PA_i) (RD_j')\Big] + \Big[(1-PA_i) (RD_j)\Big]$$

hence,

$$(11) \quad \overline{EP}_{ij} = 2 (\overline{RD}_{ij}^2 - SP^2)^{\frac{1}{2}}$$

To summarize, a series of equations have been developed
to account for the effect of several variables on the width of
the path a trout will sweep along the sediment when it searches
for different prey. These components comprise the reactive
distance submodel (fig. 5). The major equations derived in
this section are:

Figure 5. A schematic flow diagram of the parameters and
    computational steps in the attack model. The components
    designated by (A) comprise the prey vulnerability submodel;
    those designated by (B) comprise the reactive distance
    submodel. The subscript (j) refers to a class of prey,
    defined according to their size and inherent contrast, of
    species (i). The parameter names are listed in Appendix I.

B   A

```
Sigma ─────┐        ┌─────────┐   ┌────────┐
           │        │    T    │   │  D(i)  │
  R  ──────┤        └────┬────┘   └────┬───┘
           │             │             │
           │    CO(i)    │   ┌─────────▼──┐
 S(j) ─────┼──────┐      └──►│   VD(i)  ◄─┘
           │      │          └─────┬──────┘
 PA(i) ────┘   ┌──▼──────┐         │
               │ EP(i,j) │         │        P(i,j)
               └──┬───┬──┘         │          │
                  │   ▲            │          │
                  │   │   ┌────────▼──┐       │
                  │   │   │  VD(i,j) ◄─────────┘
                  │   E   └─────┬─────┘
                  │             │            V Y
                  │             │             │
                  └────────────►│             │
                       ┌────────▼──┐          │
                       │  RE(i,j) ◄────────────┘
 RS(i) ───────────────►└────┬──────┘
                       ┌────▼──────┐
                       │  RA(i,j)  │
                       └────┬──────┘      CS(i)
                       ┌────▼──────┐        │
                       │  RC(i,j) ◄──────────┘
                       └────┬──────┘
                          ┌─▼─┐
                          │ Σ │
                          └─┬─┘
                       ┌────▼──┐
                       │ RC(i) │
                       └───────┘
```

SP
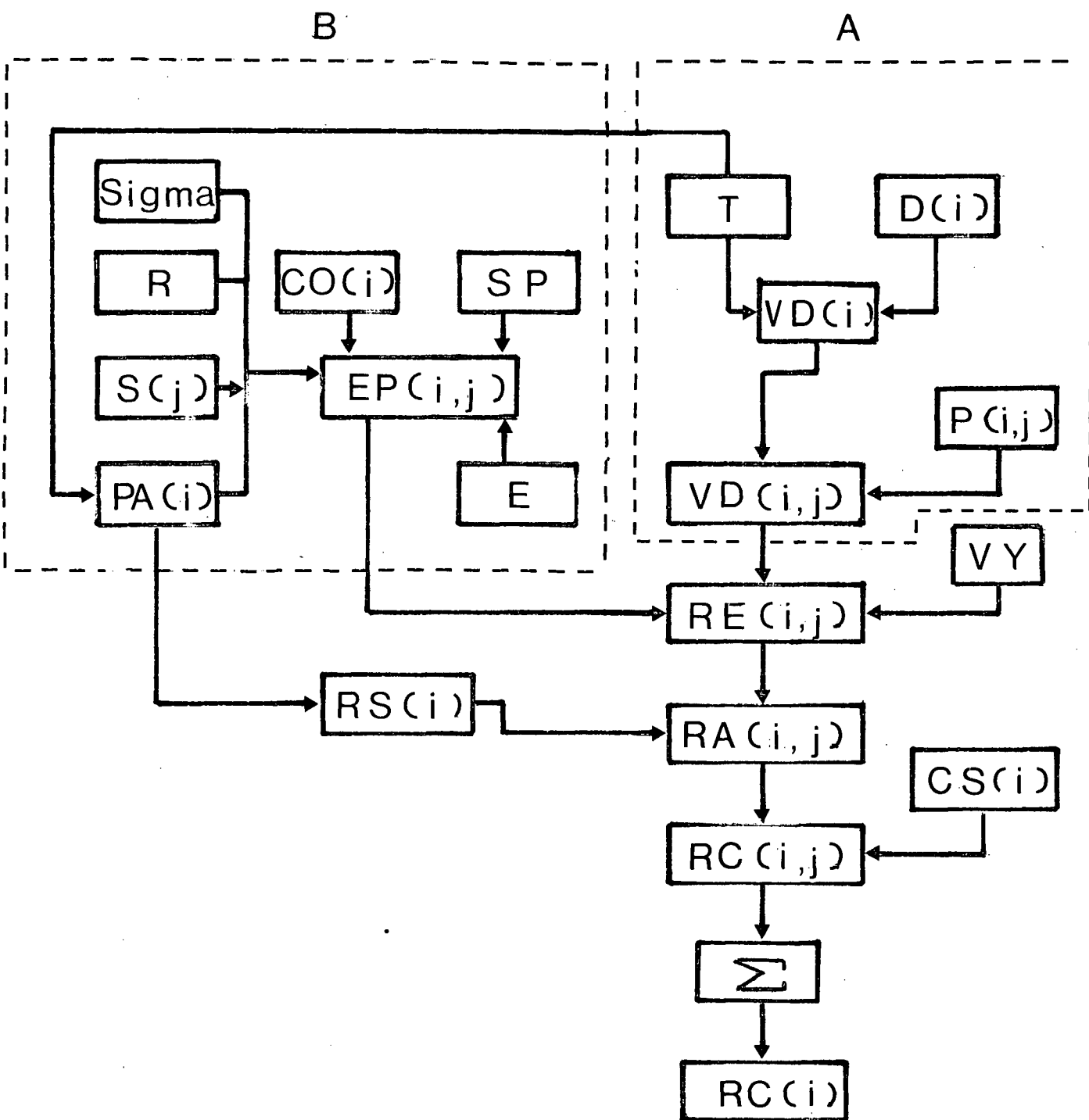
TABLE 5. Values for the parameters of the attack model. (*) indicates an estimated value. In the case of the illumination (R) the value chosen represents the estimated value of (R_{max}) for trout (after Ali, 1959).

Parameter	Crangonyx	General	Hyalella	Source
A		0.356		Hester, 1968
B		0.210		Table 1
C_o	0.14	0.14	0.14	*
CM		0.22		*
CS		0.84		Section I
CT_{min}		0.05		Hester, 1968
E		0.23		Table 4
K_1		0.25		*
L		0.19		Table 1
M3	0.138		0.180	Section III
M4	4.63		5.13	Section III
M5	0.39		0.01	Section III
M6	0.069		0.039	Section III
M7	0.0033		0.0017	Section III
MC		0.22		Figure 3
R_{min}		0.001		Ali, 1959
R		1.0		*
RS		0.39		Table 3
RS'		0.74		Table 3
6 (Lake)		0.91		Hargraves, 1969
S_{min}		5.0		Table 2
SP		0.10		Section I
VY		10.0		*

the attenuation of prey contrast,

(1) $\quad C_a = C_o e^{-(6) X}$

the apparent contrast required to elicit an attack,

(5) $\quad CT = K_1 e^{-\left[(A) R\right] + \left[L - B(\ln(S))\right]}$

The distance (X) which satisfies the equality ($C_a = CT$) can be found by solving (1) and (5). This distance is then defined as the reactive distance (R_j) for a stationary prey of size and contrast (j). The effect of prey motion is given by,

(6) $\quad R_j' = R_j + MC.$

However, if the background is broken, then the distance of reaction is:

(7) $\quad RD_j = (R_j)E$, if the prey is stationary

or

(8) $\quad RD_j' = (R_j')E$, if the prey is moving.

Finally, the width of the path of search was expressed as:

(11) $\quad \overline{EP}_{ij} = 2 (\overline{RD}_{ij}^2 - SP^2)^{\frac{1}{2}}$

THE ATTACK MODEL

Holling (1966) has shown that 4 basic components determine the rate predators capture prey, they are:

1) the density of vulnerable prey,

2) the width of the path of search,

3) prey recognition and capture success, and

4) the predator's velocity.

The seasonal changes in the density of vulnerable amphipods in Marion Lake (Section III) and the width of the path of search have already been considered; the remaining aspects will be treated in this section as the attack model is synthesized.

The velocity at which trout search for food was determined earlier (Section I) and was found to average about 4 cm/sec. Although this parameter was measured in an artificial situation, field observations verified that trout do search slowly and that a velocity of 4 cm / sec. is not an unreasonable estimate. These observations, however, also indicated that trout frequently shift their vertical position and do not maintain a specific pattern of search for any length of time. The result of this sporadic hunting behaviour is that in the course of an hour a fish may effectively search only 10 linear meters of sediment. Although this is a rather crude estimate of the average velocity of trout in the field it is assumed to be reasonable value.

Depending upon the type of background and the relative activity of different prey, trout will successfully discover only a relatively small proportion of animals that are actually within the path they sweep along the sediment. Their average success in recognizing prey ($\overline{RS}_i$) can be estimated by weighting this component with respect to the proportion of animals that

are active (PA_i) and the ability of trout to recognize both moving and non-moving prey. In which case,

$$(14) \quad \overline{RS}_i = \left[(PA_i) \ (RS') \right] \ + \ \left[(1-PA_i) \ (RS) \right]$$

where (RS') and (RS) are respectively, the probabilities that a predator will recognize a moving and stationary target (Table 3).

One final component remains to be considered and that is capture success. This fragment represents the probability that a prey will be successfully approached to within striking distance and then captured (Holling, 1966). Trout are 100% successful in approaching both Hyalella and Crangonyx, and on the average 84% of the strikes they attempt capture prey (Section I). This is consistent with the general observation that predators which pursue prey tend to be very successful in subduing relatively slow moving, or stationary animals (Holling, 1966; Messenger, 1968) but not necessarily faster moving targets (Dixon, 1959; Braum, 1967). In Marion Lake, most of the benthic-living invertebrates are less than 15 mm in length and are fairly slow moving, therefore, the component of capture success can be added to the attack model and treated as a constant. In which case, the rate of prey capture (RC_{ij}) can be derived by combining the prey vulnerability (Section III) and reactive distance submodels with the searching velocity (VY), prey recognition

($\overline{RS}_i$) and capture success (CS) components. The result is,

$$(12) \quad RC_{ij} = \left[\overline{EP}_{ij} \quad (VY) \quad VN_{ij}\right] \overline{RS}_i \ CS$$

This step completes the attack model. As it stands, it is not a complete description of the predation process because it does not consider the amount of time trout spend handling food, the effect of hunger motivation, or learning. These aspects have been shown to affect their feeding behaviour (Section I and II). Nevertheless, the purpose of this section is to test the concept that the selective exploitation of amphipods, as well as several other invertebrates, can be explained at the perceptual level. This model subsequently accomplishes this aim.

APPLICATIONS OF THE MODEL

The selective Exploitation of the Amphipods, Odonates, Planorbids and Caddis.

A previous examination of fish stomachs (Efford and Tsumara, unpublished data) indicated that throughout most of the year trout feed extensively upon benthic invertebrates. Four major groups, the amphipods, the odonates, the caddis (principally Banksiola crotchi) and the planorbids (Menetus and Helisoma), account for about 60% of the total energy input to the trout population. These four groups can therefore

be singled out as the most important prey. Some data on the average density and size of each of these animals, other than the amphipods, are briefly summarized for several selected months in Table 6.

Although there is little quantitative information concerning their vertical activity, there is some evidence which suggests that the odonates and caddis tend to live at the mud-water interface, or can be found in areas of vegetation. Neither of these invertebrates appear to burrow into the sediment. The planorbids, on the other hand, will move below the mud-water interface and may have an activity pattern that is somewhat similar to the amphipods (Delury, personal communication). Guided by these rather limited observations, I have assumed that the planorbids have a vertical activity pattern that is identical to Hyalella, but that the odonates and caddis always remain exposed. I have also assumed (on the basis of some data) that the caddis spend most of the time moving, while the planorbids and odonates are relatively inactive.

The equations developed above were transcribed into Fortran and a computer simulation was conducted to predict the rate each of these prey could be captured by trout. These results were then compared with the actual pattern of exploitation that was observed during the months of February, May, June, August and November. These were the only months in which stomach samples were taken from the trout population (Efford and Tsumara, unpublished data).

TABLE 6. The population characteristics of the odonates, caddis and planorbids for several selected months during an 'average' year. (MD) is the mean density (no./sq. m.), (ML) is the mean length (mm) and (PA) is the instantaneous proportion of prey that are active.

	Prey Group								
Month	Odonates (1)			Caddis (2)			Planorbids (3)		
	MD	ML	PA	MD	ML	PA	MD	ML	PA
Feb	10	10	0	9	7	1	40	4	*
May	4	12	0	4	10	1	63	5	*
June	5	10	0	4	10	1	63	5	*
Aug	4	8	0	1	10	1	57	5	*
Nov	5	11	0	7	10	1	50	4	*

* assumed to follow the same activity pattern as Hyalella.

Data Sources

(1) Pearlstone (pers, com.); Hamilton (1965).

(2) Winterbourn (pers, com.)

(3) Lee (1967)

In the simulation the water temperature (Appendix II), density and average size of each prey (amphipods, Appendix III; remainder, Table 6) were changed to correspond to the average condition of each of these variables during the period in question. The other parameter values required in the model are summarized in Table 5. At each time interval the model simulated the rate trout could capture different prey by searching for one hour. The predicted occurence of food organisms (expressed as a percentage) was calculated from these results.

Table 7 A presents a comparison between the observed exploitation and an expected distribution that is based upon the premise that trout capture prey in direct proportion to their abundance. There is little doubt that there is an extremely poor correlation between the observed and expected distributions, especially for the amphipods and caddis. Therefore, at least during these months, the trout population was feeding selectively.

The pattern of exploitation that was predicted by the simulation is shown in Table 7 B. In this case there is considerably better agreement between the observed and predicted occurence of prey. Part of the explanation why the simulation was more accurate in accounting for the frequency of amphipods and caddis is that it took into consideration their vertical dispersal behaviour, their average size and activity.

TABLE 7 A. A comparison between the expected and observed percentage occurence of different prey groups in trout stomachs. The expected (E) distribution assumes that each prey was exploited in direct proportion to its density. (O) is the observed distribution of prey.

Month	Amphipods		Caddis		Odonates		Planorbids	
	O	E	O	E	O	E	O	E
Feb	7	95	47	0.8	7	0.8	38	3
May	49	90	34	5	7	5	9	8
June	70	90	10	0.6	7	0.6	14	7
Aug	38	96	16	0.1	9	0.2	39	3
Nov	20	96	51	0.4	25	0.3	4	3
	57%[a]		31%[a]		10%[a]		16%[a]	

[a] Mean deviation from observed

TABLE   7 B.   A comparison between the observed (o) and
predicted (P) percentage occurence of different prey groups
in trout stomachs.   The predicted distribution was generated
from the simulation model.

Month	Amphipods		Caddis		Odonates		Planorbids	
	O	P	O	P	O	P	O	P
Feb	7	21	47	48	7	30	38	1
May	49	50	34	30	7	17	9	2
June	70	70	10	16	7	9	14	4
Aug	38	94	16	2	9	2	39	22
Nov	20	22	51	56	25	20	4	2
	14%[a]		6%[a]		9%[a]		18%[a]	

[a] Mean deviation from observed

For example, the amphipods are relatively small, spend a great deal of time concealed and are only moderately active when exposed. These characteristics will tend to lower their vulnerability to attack. On the other hand, the caddis are large, totally exposed and tend to spend most of the time actively moving; hence, they are more vulnerable than one would expect simply on the basis of their density.

The simulation did not account for the occurence of the planorbids very accurately. In this case, it is probable that the vertical and horizontal activity of this group is important and should be examined in further detail. In addition, the possibility that trout learn to selectively detect planorbids can not be overruled (Section II). Nevertheless, since there is considerably more information concerning the behaviour of Crangonyx and Hyalella the exploitation of these populations can be explored in more detail.

The Size Selective Exploitation of Amphipods

There are three specific characteristics to the pattern of exploitation of amphipods by the trout population in Marion Lake. The first, is that different size categories of Hyalella and Crangonyx are not consumed in direct proportion to their abundance. Secondly, even though Hyalella is about 7 times more numerous than Crangonyx, the latter is captured slightly more frequently. Finally, the exploitation of both species changes seasonally, becoming more pronounced in the summer and

falling to a lower level in the spring and late fall. The
question is, can the model account for any of these observations
and if so, what are the major factors involved?

In the simulation conducted for amphipods, an 'average'
year was divided into 24 two week intervals. At the beginning
of each period the ambient water temperature (Appendix II),
the density of both species (Appendix III) and the size composition
(considered in size classes of 1 mm) were changed to follow
the average trend in each of these parameters. The other parameter
values for the model are listed in Table 5.

The positive relationship between the width of the searching
path and prey size implies that large prey should be more
vulnerable to attack than smaller individuals of the same species.
In addition, depending upon the average distance trout search
from the sediment they may not detect some small size classes
of amphipods. Therefore, these two characteristics suggest
that trout should disproportionately attack large prey but are
not likely to attack others below a critical size.

Figure 6 shows the frequency of different size classes of
Hyalella captured in the months of June and November. These
periods were selected because the greatest number of trout
stomachs were taken. In this figure, the expected curves
indicate the number of animals that should have been found if
each size class was exploited in proportion to its abundance.

The observed distribution demonstrates that large Hyalella
were captured more frequently than one would expect and that
animals less than 3 mm were not found at all. The predicted
frequency curves were calculated by multiplying the actual
number of Hyalella that were found by the ratio each size
class was predicted to be captured.

In both months (fig. 6) there was a significant difference
between the observed and expected distributions ($X^2$0.05) which
indicates that the trout were selectively exploiting different
size classes of prey. On the other hand, the simulation
predicted that Hyalella less than 3 mm should not have been
found in trout stomachs and was able to account for the
occurence of other size classes of prey to the extent that
observed and predicted distrubtions are not significantly
different.

A similar comparison of the observed, predicted and expected
size composition of Crangonyx is presented in Table 8. In
this case, the fit of the predicted distribution is not as
close as it was for Hyalella but is still not significantly
different from the observed. Although the simulation predicted
that 2 mm was the smallest size class of Crangonyx that trout
could detect, this supposition could not be tested because
during the months in which stomach samples were taken, all the
Crangonyx in Marion Lake were greater than 2 mm in length.

In any case, it appears as if the relationship between
prey size and reactive distance, as well as the propensity of

Figure 6. A comparison of the observed (solid circles),
    expected (solid triangles), and the predicted (open
    circles) distribution of different size classes of
    Hyalella found in trout stomachs at two different
    sampling periods. See text for further explanation.
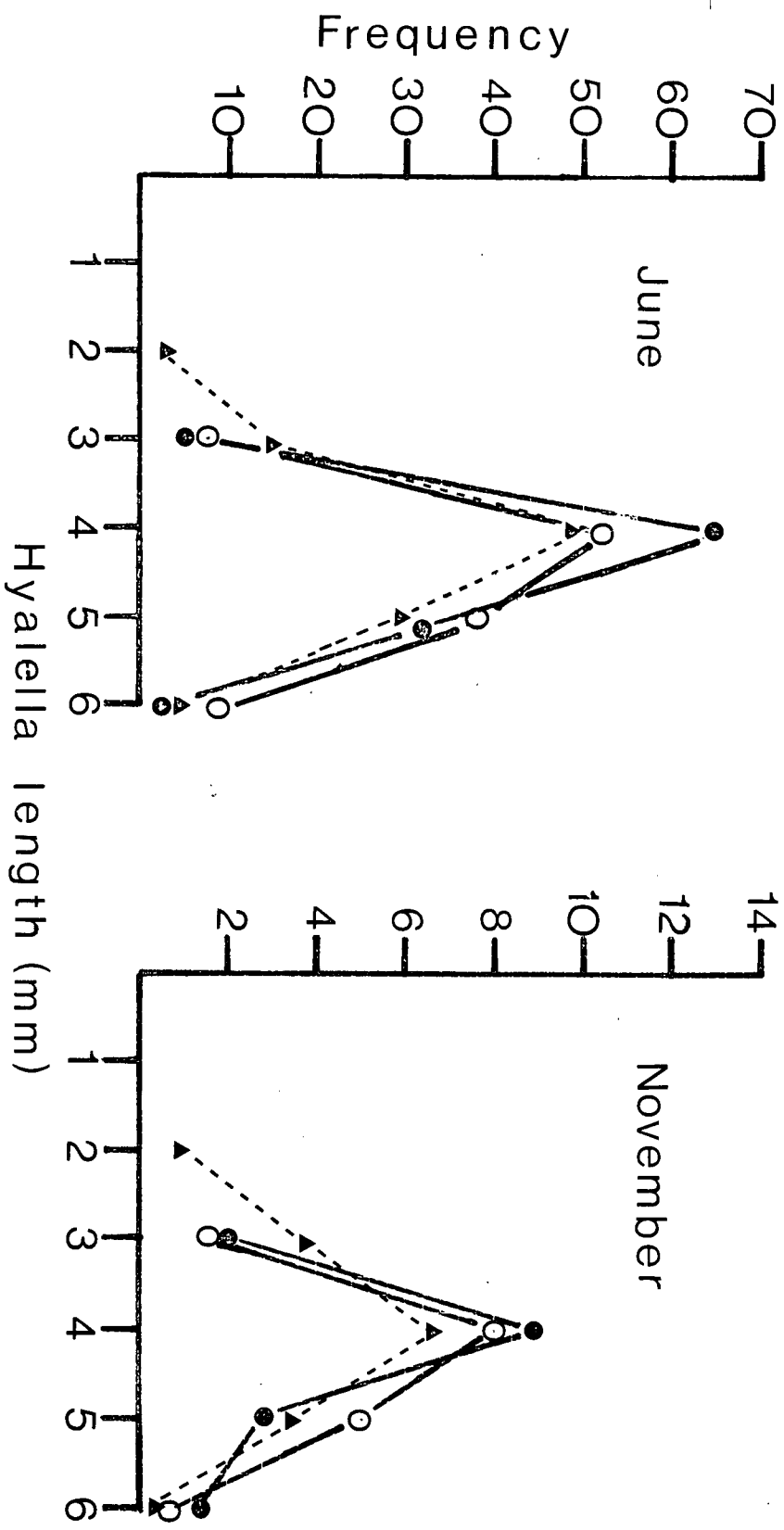
TABLE 8. A comparison of the fit between the expected (E), predicted (P) and actual (O) size composition of <u>Crangonyx</u> found in trout stomachs in the month of November. The expected number is based upon the assumption that trout were capturing different size classes in direct proportion to their respective field densities. The predicted number is based upon the results of a simulation.

Size class (mm)	Number (O)	Number (P)	Number (E)
4	0	0	0
5	2	1	1
6	2	9	11
7	10	10	11
8	12	8	7
9	9	6	6
10	2	4	3
11	4	2	1

Chi-squared (O - P) = 7.4

Chi-squared (O - E) = 11.2 *

* Significantly different at 0.05 level

trout to maintain a searching position are sufficient mechanisms

to account for their selective exploitation of large amphipods

and the existence of a threshold or minimum size of prey they

can detect.

Seasonal Changes in the Exploitation of Amphipods

The number of amphipods a trout could capture, at different

times of the year, by searching for one hour, is presented in

Figure 7. This simulation shows that the vulnerability of both

species does not reflect changes simply in their seasonal

abundance. For example, Crangonyx reaches a peak density at

the end of June (Appendix III), and yet is most vulnerable to

attack early in September. The same is true for Hyalella, it

is most abundant at the end of August, but apparently is more

vulnerable to attack approximately one month later. Moreover,

although Crangonyx is always less numerous than Hyalella, the

simulation suggests that both species are just as vulnerable

to capture throughout most of the year, except in the late

part of the summer (July and August). At this time, Crangonyx

is considerably more susceptible.

For each month in which samples were available, the stomach

contents of the trout were analysed with respect to the average

number of Crangonyx and Hyalella that were found in the gut.

These data are superimposed over the simulated vulnerability

curves in Figure 7. With the exception of the April sample,

the observed trend in exploitation closely follows the simulated

Figure 7. A comparison of the simulated (curve) and
    observed (data points) trend in the exploitation of
    Crangonyx and Hyalella, by trout, in Marion Lake.
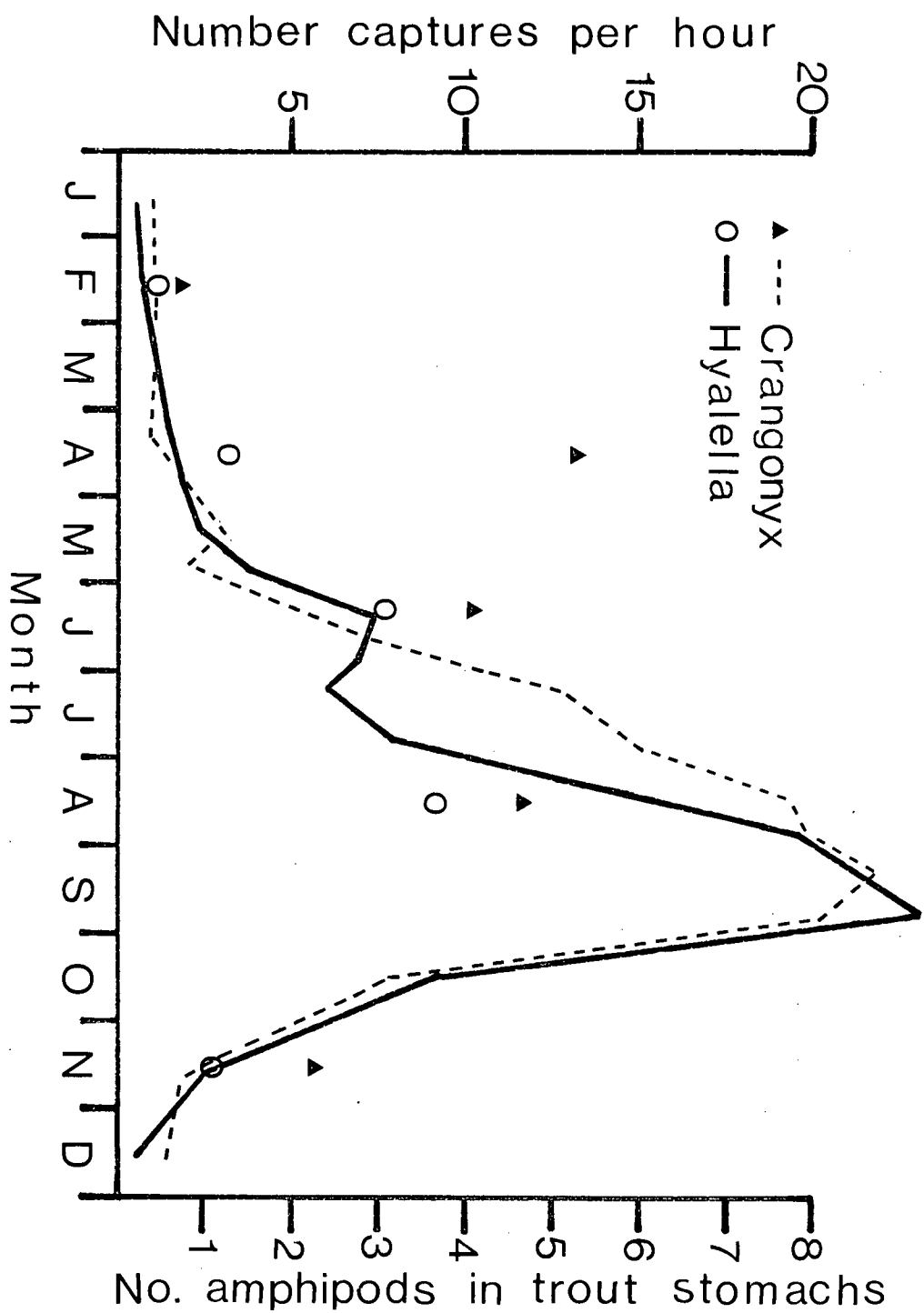
trend. A comparison of these results also shows that Crangonyx
was predicted to be just as vulnerable to capture as Hyalella
which, with one exception, did in fact occur.

Therefore on the basis of these data it seems as if the
simulation model can account for the seasonal pattern of
exploitation as well as the fact that Crangonyx is captured
just as frequently as Hyalella. Evidently, the characteristics
of prey, namely, their size and relative activity contribute
significantly to determining the risk of predation. These
characteristics can apparently be important enough to override
considerable differences in density.

DISCUSSION

One of the advantages of developing models of biological
processes such as predation is that one can examine the apparent
importance of different components. Any resulting inferences
can then be expressed as hypotheses and tested either experimentally
or in the field.

For example, the distance trout can detect prey of a specific
size and inherent contrast is dependent to some extent upon
the turbidity of the water (6). If the extinction coefficient
of the water were increased then the reactive distance would
diminish, simply because trout would have to be closer to prey
in order to detect the contrast threshold for discrimination.
Subsequently, all else being equal, in murky waters visual
predators will attack prey at a slower rate than they could

in clearer water. The question which arises however, is just how significant is the clarity of the environment to predation?

The simulation model was able to account for the exploitation of amphipods as well as several other prey, therefore, it may be a reasonable abstraction of the feeding behaviour of trout. If this is the case then it is worthwhile to examine the sensitivity of the model to some of its components.

Table 9 presents the change in the vulnerability of Crangonyx and Hyalella that resulted when several components were altered. In conducting these simulations, I arbitrarily increased the value of each parameter by 10% of the estimated 'real' value (Table 5). The difference in the rate of capture each of these attendant changes produced indicates the sensitivity of predation to these parameters. The components of the predation model can be partitioned into 3 categories: 1) environmental characteristics, 2) prey characteristics, and 3) predator characteristics.

Environmental Characteristics

To answer the question raised earlier, the vulnerability of Crangonyx and Hyalella is relatively insensitive to the turbidity of the water; a change in (6) was not as important as an increase in either the ambient illumination or temperature (Table 9).

Despite the fact that the searching activity of a visual predator will be restricted by the level of illumination, even at levels above the limit of vision (R_{min}) the illumination could

TABLE 9. Sensitivity of the attack model to selected parameters. Each parameter was increased by 10% of its 'real' value (Table 5.). In the case of the learning component, the width of the path of search was doubled. The period of simulation was the January 1-15 interval.

Parameter	% change in the attack rate	
	Crangonyx	Hyalella

A. Environmental Characteristics

Parameter	Crangonyx	Hyalella
Temperature (T)	22	33
Illumination (R)	22	20
Turbidity (6)	- 2	- 5

B. Prey Characteristics

Parameter	Crangonyx	Hyalella
Inherent Contrast (C_0)	43	128
Vertical Activity (M3)	22	24
Horizontal activity (M7)	17	14

C. Predator Characteristics

Parameter	Crangonyx	Hyalella
Learning	50	50
Recognition Success (RS)	22	24

indirectly influence the searching pattern an animal adopts.
Hamilton (1965) and Hyatt (personal communication) found that
in the late summer (August), the trout population in Marion
Lake, displays a distinct diel feeding pattern. In the early
morning (0500 to 0900 hrs) most animals appear to be feeding
predominantly in the water column on chironomid pupae.
Throughout the rest of the day, however, some fish will shift
their position and hunt sporadically for benthic prey. By
the late afternoon (2000 hrs) most of the population will have
shifted back to feeding in the water column until 2300 or 2400
hrs. After this time the population may become relatively
inactive since there is a general decline in the amount of food
trout contain in their stomachs.

The foraging activity, of trout, in the water column
closely coincides with the diel migration of chironomid pupae
into this region. Little migration occurs during the day
(Hamilton, 1965). As a result, the general shift in the feeding
position of the trout population could be in response to changes
in the availability of food in different sectors of the environment.
During periods of low illumination (early morning and late
evening) trout will not detect prey on the lake bottom as
effectively as they can in the water column. An object contrasted
against the evening sky will present a higher level of contrast
than a similar target on the sediment (Hester and Taylor, 1965).
Therefore, trout should be able to feed on limnetic prey at
lower levels of illumination than they require to hunt for

benthic-living animals. As the level of illumination rises,
however, and the migration of chironomids begins to subside,
the population may be able to feed more efficiently on the
lake bottom; in which case, their attention could be shifted
to this region. This supposition was suggested by earlier
experiments (Section I) which demonstrated that trout will
not maintain a searching pattern unless they are reinforced
above a critical rate (about 2 captures per minute).

Changes in the ambient temperature can also be expected
to influence the vulnerability of prey such as amphipods. In
this case, rising temperatures will increase the number of
animals that are exposed as well as the level of activity of
exposed individuals (Section III). Therefore trout will be
more successful in recognizing these prey and will attack from
a greater distance. The major role that water temperature plays
in the interaction between the trout and the amphipods in
Marion Lake is apparent in Figure 7. The vulnerability of
both Crangonyx and Hyalella is closely correlated with the
seasonal temperature pattern (Appendix II).

In general, seasonal and diel changes in the water
temperature and the ambient illumination may well be two of
the most important factors that affect the activity of aquatic
animals (Fry, 1947; Thorne, 1969) and subsequently their
vulnerability to predation.

Prey Characteristics

The sensitivity analysis (Table 9) indicates that several physical and behavioural characteristics of prey will also affect the rate of capture. Hyalella and Crangonyx spend much of the time concealed either in the sediment or under objects at the mud-water interface. In this respect, the behaviour of these species is similar to other aquatic invertebrates (Berglund, 1968; Straskraba, 1965). As a result at any instant in time only a small proportion of prey will be susceptible to attack from visual predators. Several authors (Allen, 1941; Huruska, 1961; Grimas, 1963) have suggested that concealment behaviour would greatly diminish the risk of a species to attack. This inference is supported by the experimental results and the simulation.

Prey vulnerability will vary seasonally, however, and perhaps even during the day depending upon a number of other factors such as 1) alterations in activity patterns, 2) changes in population density and, 3) changes in the size composition of the population. The effect of a sudden shift in the size structure of a prey population on the rate of predation is illustrated in Figure 7. In this example, the simulated vulnerability curves for Crangonyx and Hyalella begin to rise in March and April in response to the increase in the ambient lake temperature. This rise continues until the latter part of May when the vulnerability of Crangonyx suddenly drops. The same phenomenon is apparent for Hyalella except that it occurs latter in June. In both cases the decline

in the rate of capture is due to reproduction and the
appearance of juveniles in the population. Although the
vulnerability of Crangonyx was not depressed for very long,
the vulnerability of Hyalella did not begin to rise again
until about one month after the onset of breeding.

In addition to the importance of concealment behaviour
and size, the inherent contrast of a prey will also affect
its risk of being attacked. In the sensitivity analysis, a
10% increase in contrast markedly raised the vulnerability
of Crangonyx and Hyalella, but especially the latter. Although
it is well known that cryptic animals are less susceptible to
being discovered by visual predators than more conspicuous
species, the sensitivity of the model to contrast demonstrates
just how important this component could be to predation.

In the sensitivity simulation, Hyalella proved to be
more responsive to a change in almost every parameter that was
investigated. Since most of these alterations changed the
reactive distance component, this would tend to have a
significant effect on a small animal due to the form of the
relationship between reactive distance and prey size (fig. 2).
In addition, a change in the distance of reaction will become
considerably amplified because it will affect the rate trout
encounter every size class of prey. Therefore, seemingly
minor changes in some major components can have a significant
effect on prey risk, especially in the case of a small animal.

Predator Characteristics

One of the most important characteristics of the feeding behaviour of trout is the fact that they maintain a position some distance from the sediment when they hunt for food. It was mentioned earlier, that if the height of the searching position ever exceeds the distance of reaction then trout will fail to discover some small size classes of prey. This characteristic was sufficient to explain why Hyalella less than 3 mm were not captured (fig. 6). In general, the propensity of trout to maintain a searching position will tend to favour a small animal, such as Hyalella, because throughout the year there will always be animals in the population that are less than the threshold size. In contrast, larger prey like Crangonyx, will have size classes invulnerable to predation only during periods of reproduction.

Under certain conditions trout can increase their responsiveness to prey (Section II). The attack model is formulated on the basis that the predator it simulates was conditioned to recognize amphipods. Since an animal that is not conditioned will react from half the distance that a conditioned trout will, the effect of learning can be simulated by doubling the width of the path of search. Obviously, if a predator can increase the area about it in which it will respond to prey, it will be able to discover food at a substantially greater rate than one that is less responsive (Table 9). Several experimental studies have verified that learning is an extremely advantageous process through which predators could

increase their rate of energy intake (Beukema, 1968; Croze, 1970).

Several characteristics of the behaviour of trout, namely, 1) their visual response to prey, 2) the dependence of their pattern of search on a threshold rate of capture, and 3) the fact that they can learn to alter their response to prey, imply that they are admirably adapted to forage in different environments. For example, they can feed on either limnetic or benthic living organisms as well as on the drift in streams. However, the fact that they maintain a searching position when they hunt over a substrate and respond to prey visually suggests that they are better adapted to feeding in the water column. Since water essentially presents a 'smooth' background, trout will maximize the area of their reactive field and will be most successful in recognizing prey when they hunt in this sector of the environment. If they feed on benthic-living prey then their hunting efficiency will be somewhat diminished, largely because the background in this case will be relatively more 'broken'. Thus they will be less successful in recognizing food and must be closer before they attack. Moreover, since they maintain a searching position they may not discover some small size classes of prey.

In any case, whether trout feed in the water column or over a substrate, they are likely to converge temporarily into areas in which food is relatively more abundant because their pattern of search is dependent upon a threshold rate of capture (Section I). In addition, the characteristic of learning will enable individuals to increase their responsiveness to prey and thereby further improve their hunting efficiency.

In conclusion, the predictions generated by the simulation model do not refute the hypothesis that the selective exploitation of Crangonyx and Hyalella, by the trout population in Marion Lake, can be explained by the process of prey recognition and detection. This hypothesis was expressed in the attack model and appears to be sufficient to account for the disproportionate exploitation of different size classes of prey as well as the observation that Crangonyx is just as vulnerable to attack as Hyalella despite a 7 fold difference in their densities. There are two principal reasons why Crangonyx is more vulnerable to attack; in the first place, it is a larger animal and secondly it spends considerably more time moving when exposed. Therefore it will be recognized more successfully and attacked from a greater distance than Hyalella.

The attack model was also able to replicate the seasonal pattern in the vulnerability of amphipods. The explanation in this case is primarily due to the seasonal change in water temperature. Very few amphipods are exposed and moving over the sediment in the winter months. However, as the water temperature rises more animals will be exposed and considerably more active. Therefore the vulnerability of both populations will rise since trout will be more successful in recognizing these prey and will discover them from a greater distance.

This study, therefore, demonstrates that due to the interaction between the behaviour of a visual predator and

the characteristics of its prey, predation is not only
affected by the density of a food organism, but also will be
influenced by its size, activity and contrast. These
factors are likely to be just as if not considerably more important
than density.

SUMMARY

1. In order to test the hypothesis that the process of prey
    detection and recognition is sufficient to explain the
    selective exploitation of prey by trout, a study was
    conducted to identify some of the factors that affect
    their visual discrimination.

2. The distance trout will react was found to be non-linearly
    related to prey size. A general system of equation was
    developed to describe the process of visual discrimination
    in terms of the relationship between the size and the apparent
    contrast a target must have before it can be detected
    (attacked).

3. The effect of the background illumination on contrast
    discrimination was not examined. This component was considered,
    however, on the basis of results documented in the literature.

4. Rainbow trout will react to moving targets from a greater
    distance than stationary prey. Irrespective of the size of

the test prey, the effect of target motion was constant
(22 cm).

5. A 'broken' background reduced the ability of trout to
    recognize prey and significantly diminished their reactive
    distance for both moving and non-moving targets. This
    effect was incorporated by assuming that the experimental
    conditions simulated the diversity of the natural lake
    substrate.

6. A general attack model was developed to simulate the exploitation
    of several invertebrate groups (odonates, caddis and
    planorbids) but principally the amphipods, by the trout
    population in Marion Lake.

7. Although the proposed model was reasonably accurate in
    predicting the percentage occurence of the amphipods, caddis
    and odonates in trout stomachs, it was unable to account
    for the high occurence of planorbids in some months.
    Therefore, it does not offer a complete explanation.

8. An additional simulation adequately predicted the 3
    characteristics of trout predation on Crangonyx and Hyalella:

    i)   their disproportionate exploitation of different
         size classes of amphipods (the model was also
         able to account for the threshold size (3mm) or
         the smallest Hyalella consumed by trout),

    ii) the fact that Crangonyx is captured as frequently
         as Hyalella even though it is 7 times less abundant

iii) the seasonal pattern to the exploitation of both
species.

9. In general, the results of this study lead to the conclusion
that the selective pressure exerted by visual predators
will tend to favour small, cryptically colored animals, a
general reduction in activity and concealment behaviour.

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Appendix I

A LIST OF SYMBOLS FOR THE ATTACK MODEL

C_o -   Inherent contrast of prey

CS   -   Success of the predator in capturing prey it has attacked.

CT   -   The apparent contrast of a prey that is required to elicit an attack

CT_{min} -   The minimum level of contrast the predator can discriminate

D   -   Prey density (no. / sq. m.)

E   -   A proportionality constant describing the effect of the background on reactive distance.

$\overline{EP}$ -   The width of the encounter path swept along the sediment (m)

MC   -   The motion constant, the additive effect of target movement on the attack distance (m)

PA   -   The proportion of exposed prey moving at any instant in time

R_{min} -   The limit of scotopic vision (ft-candles)

R_{max} -   The lowest level of illumination which produces maximum visual acuity (ft-candles)

R   -   The level of ambient illumination (ft-candles)

RA   -   The rate of attack (no./ hr.)

RC   -   The rate of capture (no./ hr.)

RE   -   The rate of encounter (no./ hr.)

$\overline{RD}$ -   The reactive or attack distance, also the radius of the reactive field (m)

$\overline{RS}$ -   Prey recognition success

S   -   The visual angle a prey subtends with the predator (min. of arc)

6   -   The rate of attenuation of target contrast, (the extinction coefficient of the water)

Appendix I (cont.)

SP   -   The distance of the predator from the sediment, its searching position (m)

T   -   The ambient water temperature (C)

VD   -   The vulnerable density of prey (no./ sq. m.)

VP   -   The proportion of prey exposed at or above the mud-water interface at any instant in time

VY   -   The predator's average searching velocity (m/ hr.)

APPENDIX II

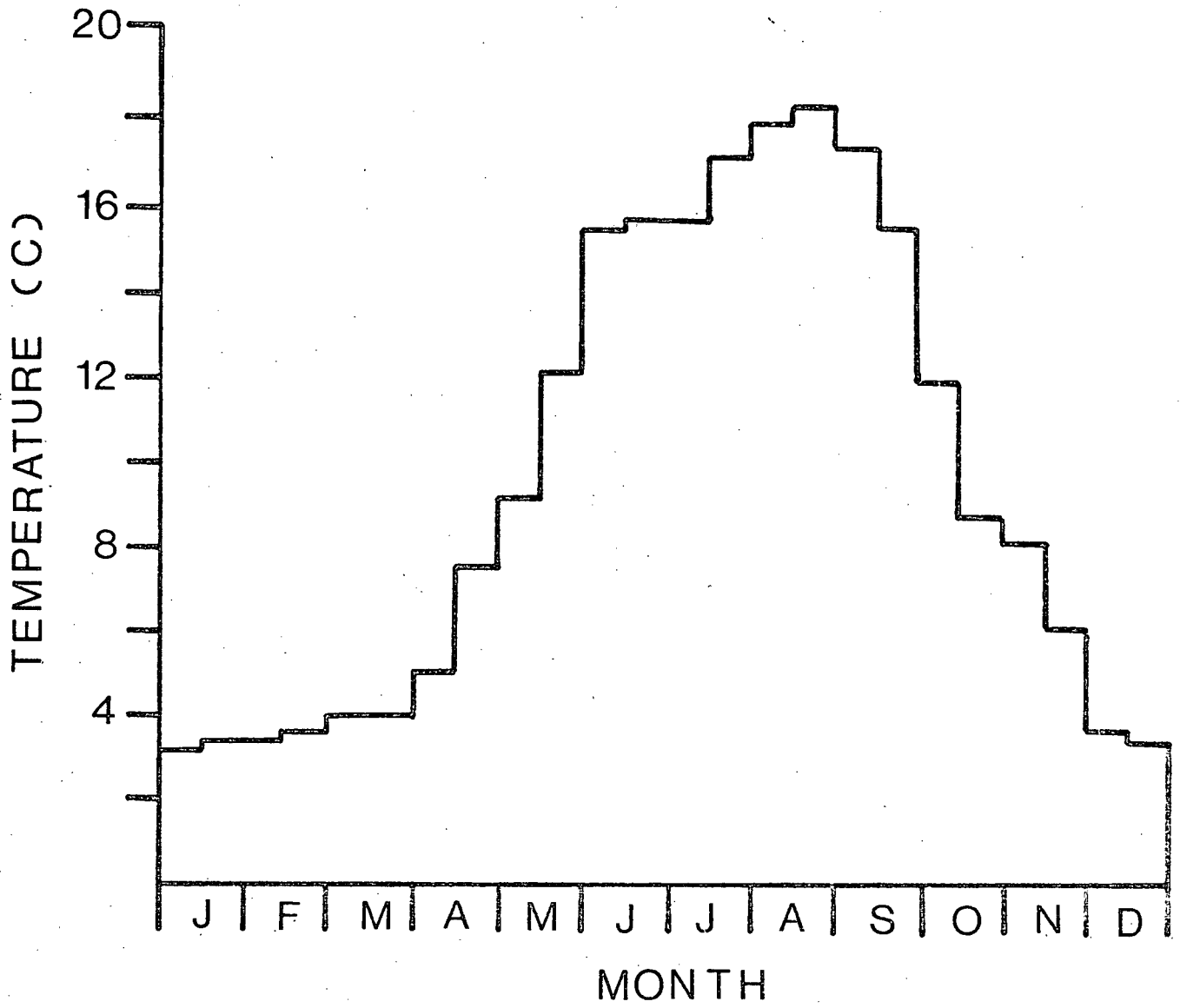THE PHYSICAL CHARACTERISTICS OF MARION LAKE

Efford (1967) and Hargrave. (1969c) presented a detailed description of the basic physical and chemical characteristics of Marion Lake. The description which follows will be confined to some of the more important features reported by these authors.

Marion Lake is a small, shallow coastal lake with a mean depth of 2.4 meters. The primary production in the water column is extremely low throughout the year. This is undoubtly due to the persistent flushing of the lake (Dickman, 1968). As a result, the turbidity of the water (extinction coefficient, 0.91; Hargrave, 1969c) is consistently high throughout the year due to the amount of particulate matter that is washed into the lake and not because of changes in the abundance of phytoplankton.

Although the lake becomes thermally stratified, all regions are subject to warming in the spring and summer. Despite fluctuations in the rate of temperature change from year to year the basic pattern is the same (fig. 1).

The sediment in Marion Lake can be basically characterized as an extremely floculent ooze (gyttja). The substrate surface however, is very diverse with respect to the size and shape of the particulate matter (stick litter, chironomid larval cases, and other material).

Figure 1. The average seasonal trend in water temperature
in Marion Lake recorded over 5 years (1963-1968) in the
region of the lake less than 3 meters.

APPENDIX III

THE POPULATION CHARACTERISTICS OF <u>CRANGONYX</u> AND <u>HYALELLA</u> IN
MARION LAKE

Several studies have been conducted on the amphipods in
Marion Lake for a considerable number of years (Hamilton, 1965;
Mathias, 1967; Bryan, unpublished data). These data indicate
that <u>Crangonyx</u> is, on the average, about 7 times less abundant
than <u>Hyalella</u> and tends to be fairly evenly distributed throughout
the lake. <u>Hyalella</u>, on the other hand, is concentrated in the
shallow littoral zone.

<u>Crangonyx</u>, the larger of the two species, generally produces
a brood of young in the summer about one month before <u>Hyalella</u>.
The timing of the reproduction of both species as well as their
relative field densities tend to be very similar from year to
year. Therefore the data from all the available sources were
pooled to establish a general description of the density (fig. 2)
and the size structure (Table 1) of each population over an
'average' year.

Figure 2. The relative density of _Hyalella_ (A) and
Crangonyx (B) in Marion Lake.
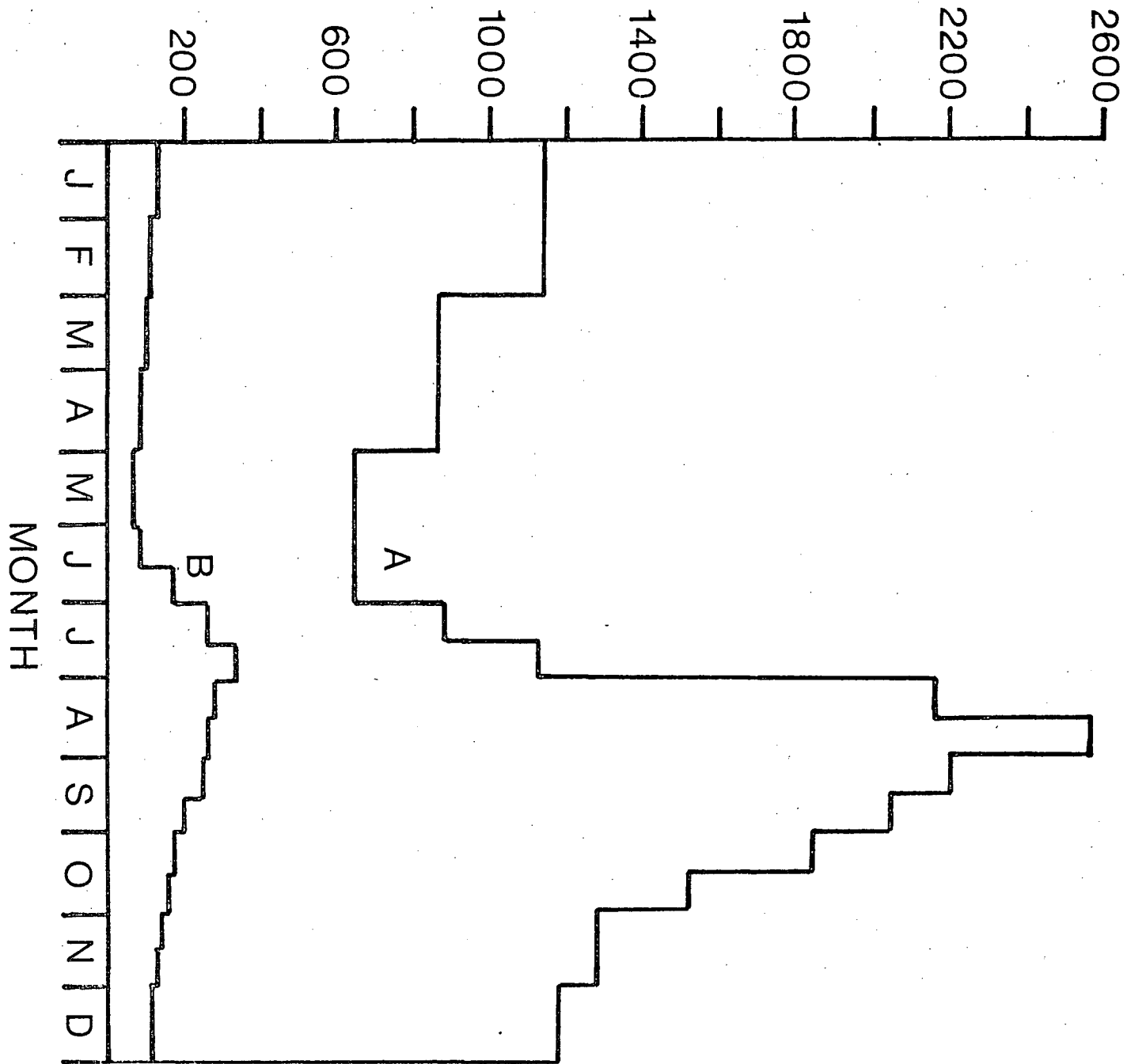
NUMBER OF AMPHIPODS PER SQUARE METER

TABLE 1.   Temporal changes in the size structure of amphipods in Marion Lake.

MONTH	Total Body Length (mm)					
	Hyalella			Crangonyx		
	L	X	H	L	X	H
Jan	2.0	4.2	5.5	5.0	7.5	11.0
Feb	2.0	4.2	6.0	6.0	9.4	12.0
Mar	2.2	4.3	6.0	6.5	9.2	12.0
Apr	2.5	4.5	6.0	7.0	9.1	12.0
May	2.5	4.5	6.5	1.0	3.7	11.0
Jun	3.5	4.8	6.0	2.0	4.1	8.0
Jul	1.5	2.5	6.0	2.0	4.5	9.0
Aug	1.5	3.1	6.0	3.0	5.7	9.0
Sep	1.5	3.7	6.5	4.0	6.3	10.0
Oct	2.0	4.1	6.5	5.0	7.3	10.0
Nov	2.0	4.1	6.0	5.0	8.1	11.0
Dec	2.0	4.2	6.0	5.0	7.6	12.0

L = lower limit to size range

X = mean size

H = upper limit to size range